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The Baetidae (Ephemeroptera) of the Comoros and Mayotte

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Abstract

Material collected in 1974 during the Austrian Hydrobiological Mission of F. Starmühlner to the Comoros and during recent years by one of the authors (NM) in the course of an ongoing freshwater monitoring program in Mayotte is the basis of this first larger study of the mayfly family Baetidae in the Comoros Archipelago (Comoros, Mayotte). We identified eight different species using morphological characters, four species on both the Comoros and Mayotte, three species on the Comoros only and one species on Mayotte only. Two species, *Dabulamanzia mayottensis* sp. nov. and *Nigrobaetis richardi* sp. nov., are new to science; they are described and illustrated based on their nymphs. The nymph of *Afroptilum bicorne* (Ulmer, 1909) is described for the first time and its assignment to this species is discussed. The description of the previously endemic Malagasy species *Potamocloeon* (*Aquaediva*) *freitagae* (Gattolliat, 2001), is complemented based on the additional material from the Comoros and re-examination of the type material. A key to the nymphs of all species of Baetidae in the Comoros and Mayotte is provided and the biogeography of the family in this region is discussed.

Keywords

Afrotropical, biogeography, COI, Comoros Archipelago, mayflies, morphology

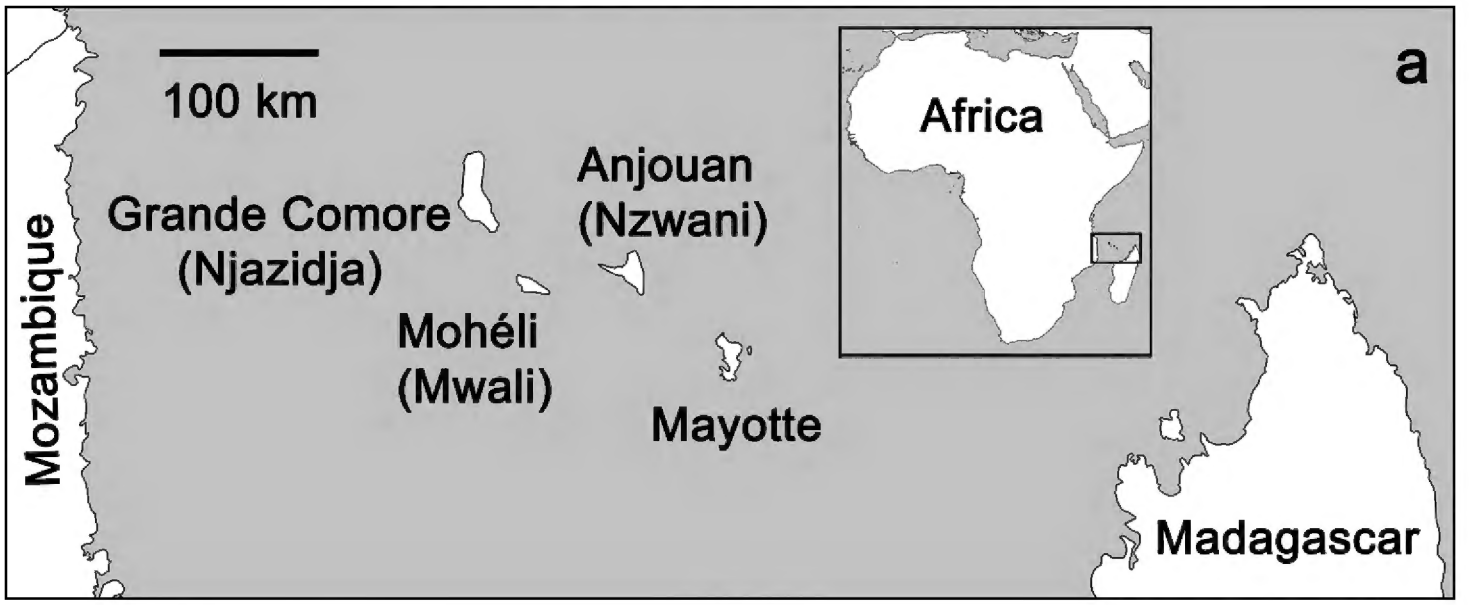
Introduction

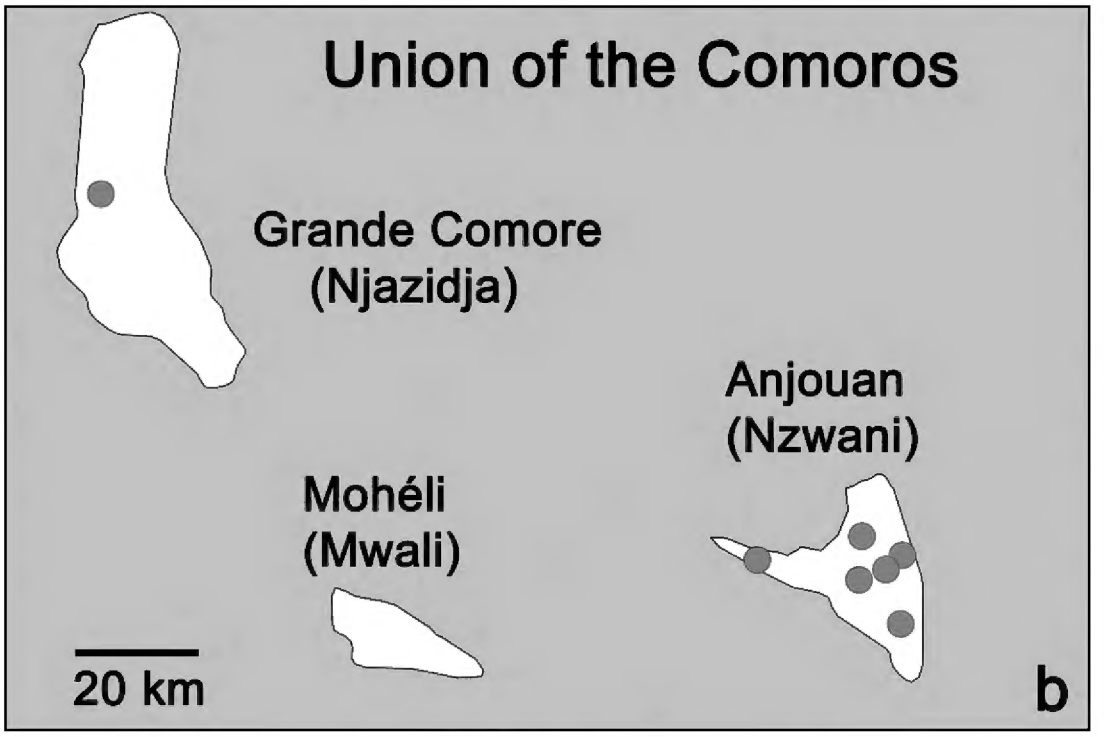
The family Baetidae has the highest species diversity among mayflies, comprising ca. 1,100 species in 114 genera (updated from Sartori and Brittain 2015; Jacobus et al. 2019; Cruz et al. 2020), which is approximately one third of all mayfly species worldwide. They have a cosmopolitan distribution except in New Zealand (Gattolliat and Nieto 2009). Investigations of the molecular phylogeny of the Order Ephemeroptera revealed the relatively basal position of the family in Ephemeroptera phylogeny (Ogden and Whiting 2005; Ogden et al. 2009; Ogden et al. 2019).

Baetidae from the south-eastern part of the Indian Ocean were subject to large scale studies. During the last 30 years, more than 50 new species and 10 new valid genera were described from the island of Madagascar, underlining the biological richness of the fourth biggest island in the world (Elouard et al. 2003). The Baetidae fauna of other islands was also studied (Mauritius, McCafferty and Mauremootoo 2001; La Réunion, Gattolliat 2004; and the Seychelles archipelago, Gattolliat 2013). The Comoros and Mayotte remain the only important area still almost unknown for Baetidae. Only a single species, *Afroptilum bicorne* (Ulmer, 1909) was briefly described at the imaginal stage from the Comoros (Ulmer 1909) and another species, *Labiobaetis glaucus* (Agnew, 1961), was reported from Mayotte (Gattolliat et al. 2018).

The Comoros archipelago comprises four principal islands, from West to East: Grande Comore, Mohéli, Anjouan and Mayotte (Fig. 1a). They are all of relatively recent volcanic origin, Mayotte forms the eastern and oldest part of the Comoros archipelago, which dates back approximately eight million years, while Grande Comore is the youngest (around 100 000 years ago). This archipelago is located at almost equidistance from Madagascar and the Eastern Coast of Africa (less than 300 km). Grande Comore is the largest island (1148 km^2) with its active volcano Mount Karthala (2361 m), followed by Anjouan (424 km^2) with its highest peak, N'Tingui (1595 m), situated in the middle of the island. Mayotte (366 km^2) is the third biggest island of the archipelago. It is composed of two main islands, Grande-Terre and Petite-Terre, the highest point is Mont Bénara (660 m) on Grande-Terre. Mohéli (290 km^2) is the smallest island, apart from the many surrounding islets (Harris and Rocha 2009). No running water occurs on Grande Comore; the only habitats suitable for aquatic invertebrates are large cisterns constructed to collect rainwater. Anjouan possesses several permanent streams. The hydrographic network of Mayotte is made up of a large number of gullies, often short in length, and about thirty perennial streams distributed exclusively and unevenly over Grande-Terre.

The upstream part of the watercourses remains relatively well preserved from human activities, which allows the maintenance of a good water quality. On the other hand, a clear degradation is often observed downstream and at the mouths of streams. Several reasons have been identified to explain this degradation: urbanization: insufficient sewage systems and many houses without connection to a





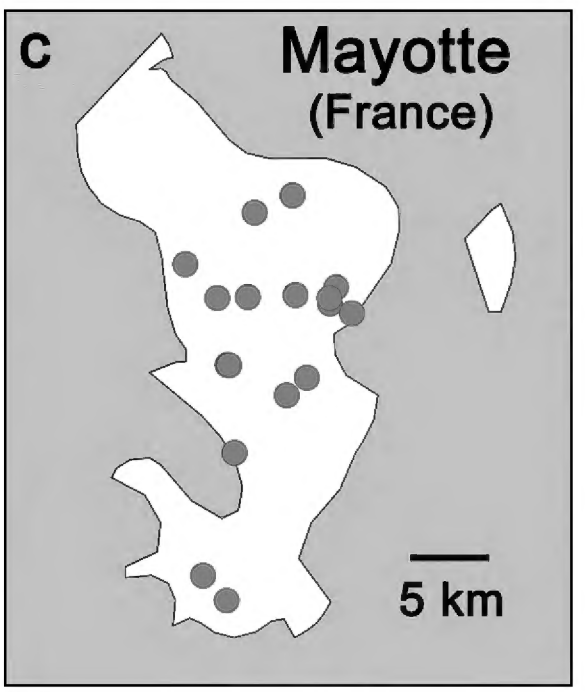


Figure 1. Maps: **a** overview of Comoros Archipelago **b** Union of the Comoros with sampled locations **c** Mayotte with sampled locations.

purification system; domestic and customary uses: traditionally, laundry is carried out directly in streams with products containing a high level of phosphates; washing cars in the rivers (hydrocarbons, used oil); this diffuse and chronic pollution leads to an increase in the pH of the water, eutrophication, and a reduction in biodiversity; industrial activities: pollution linked to limited or non-existent treatment of wastewater; agriculture: monocultures of bananas and cassava, slash-and-burn cultivation practices, or deforestation accelerate soil erosion, terrigenous transport in rivers and decrease in river flows; indirect uses: rivers collect unauthorized dumps like sachets of detergents, bottles of bleach, clothes, household waste, bulky items which all accumulate and cover the banks and beds of rivers, particularly in their downstream part. Each rainfall carries away significant amounts of waste into the waterways, and then to the sea.

The archipelago is subject to a humid tropical climate strongly influenced by the maritime environment and the direction of the winds. Two seasons are distinguished: a hot and rainy season from December to March with abundant and violent precipitation and a cooler dry season from June to September. Grande Comore, Anjouan and Mohéli are forming the Union of the Comoros, whereas Mayotte is an overseas department of France since March 2011.

In 1974, the Austrian Hydrobiological Mission collected aquatic animals in the Comoros, Mauritius, La Réunion and the Seychelles (Starmühlner 1976, 1979). Most of the sampling in the Comoros was done on the island of Anjouan and no samples were taken on Mohéli and Mayotte during the Austrian mission in 1974 (Fig. 1b). Baetidae were reported from various habitats and localities, but without additional treatments or more precise identification. Based on this material, the Leptophlebiidae of the Comoros were described (Peters 1980). The genus *Prosopistoma* Latreille, 1833, was also reported from Anjouan but no further investigation was done (Starmühlner 1976). Mayotte was subsequently well sampled within the framework of an ongoing French water-monitoring program conducted for many years by one of the authors (NM; Fig. 1c).

Here, we report eight species of Baetidae from the Comoros archipelago: four species on both the Comoros and Mayotte, three species on the Comoros only and one species on Mayotte only. Five species are new reports for the Comoros and three are new reports for Mayotte. One species from the Comoros (*Nigrobaetis richardi* sp. nov.) and one from Mayotte (*Dabulamanzia mayottensis* sp. nov.) are described and illustrated as new species, based on nymphs. The nymph of *A. bicorne* is described for the first time and its assignment to this species is discussed. The description of the larva of *Potamocloeon* (*Aquaediva*) *freitagae* (Gattolliat, 2001) from Madagascar is complemented based on material from the Comoros.

Mayotte is relatively well sampled due to the ongoing freshwater monitoring program, contrary to the Union of the Comoros, where collection activities remained geographically limited and without new sampling in the last 50 years. However, the mayfly fauna of the Comoros archipelago seems to be poorly diversified based on the results of the present study and previous ones.

Materials and methods

Specimens were collected in 1974 during the Austrian Hydrobiological Mission of F. Starmühlner to the Comoros and during recent years by one of the authors (NM) in the course of an ongoing freshwater monitoring program in Mayotte. The nymphs were preserved in 70%-96% ethanol.

The dissection of nymphs was performed in Cellosolve (2-Ethoxyethanol) with subsequent mounting on slides with Euparal liquid, using an Olympus SZX7 stereomicroscope.

The DNA of part of the specimens was extracted using non-destructive methods allowing subsequent morphological analysis (see Vuataz et al. 2011 for details). We amplified a 658 bp fragment of the mitochondrial gene cytochrome oxidase subunit 1 (COI) using the primers LCO 1490 and HCO 2198 (Folmer et al. 1994; see Kaltenbach and Gattolliat 2020 for details). Sequencing was done with Sanger's method (Sanger et al. 1977).

Drawings were made using an Olympus BX43 microscope. To facilitate the determination of the new species and the comparison of important structures with other species, we partly used a combination of dorsal and ventral aspects in one drawing (see Kaltenbach et al. 2020: fig. 1).

Photographs of nymphs were taken using a Canon EOS 6D camera and processed with Adobe Photoshop Lightroom (http://www.adobe.com) and Helicon Focus version 5.3 (http://www.heliconsoft.com). Photographs were subsequently enhanced with Adobe Photoshop Elements 13.

Approximate GPS coordinates to the older sample locations (1974) were attributed using Google Earth (https://www.google.com/earth/download/ge/) and Starmühlner 1979: fig.3. Distribution maps were generated with SimpleMappr (https://simplemappr.net, Shorthouse 2010). The coordinates of the sample locations are given in Table 1. The dichotomous key was elaborated with the support of DKey version 1.3.0 (http://drawwing.org/dkey, Tofilski 2018).

The terminology follows Hubbard (1995) and Kluge (2004).

Abbreviations

FAMU Florida A&M University, Tallahassee (USA);
MZL Musée de Zoologie Lausanne (Switzerland).

Results

List of Baetidae species from the Comoros Archipelago

1. *Afroptilum bicorne* (Ulmer, 1909)
2. *Cloeon smaeleni* Lestage, 1924
3. *Dabulamanzia mayottensis* sp. nov.

4. *Labiobaetis glaucus* (Agnew, 1961)
5. *Labiobaetis vinosus* (Barnard, 1932)
6. *Nigrobaetis richardi* sp. nov.
7. *Potamocloeon* (*Aquaediva*) *freitagae* (Gattolliat, 2001)
8. *Procloeon* (*Oculogaster*) *cylindroculum* Kimmins, 1956

Table 1. Coordinates of locations of examined specimens.

Species	Island	Location	Coordinates
Afroptilum bicorne	Anjouan	Riv. Santsa	12°17'31"S, 44°29'43"E
	Mayotte	Riv. Bouyouni	12°44'55"S, 45°08'36"E
		Riv. Dembéni (middle course)	12°51'07"S, 45°09'41"E
		Riv. Djalimou	12°57'14"S, 45°06'51"E
		Riv. Koualé (trib. forest 3)	12°47'43"S, 45°09'59"E
		Riv. M'Tsangachéhi	12°53'04"S, 45°07'55"E
Cloeon smaeleni	Anjouan	Lac Sacré, Dzialandze	12°13'30"S, 44°25'55"E
	Grande Comore	Moroni (North of)	11°38'17"S, 43°16'47"E
	Mayotte	Riv. Bouyouni	12°44'55"S, 45°08'36"E
		Riv. Dapani	12°58'05"S, 45°07'39"E
		Riv. Dembéni (lower course)	12°50'31"S, 45°10'22"E
		Riv. Dembéni (middle course)	12°51'07"S, 45°09'41"E
		Riv. Djalimou	12°57'14"S, 45°06'51"E
		Riv. Haoutoungou	12°47'49"S, 45°07'20"E
		Riv. M'Tsangachéhi	12°53'04"S, 45°07'55"E
Dabulamanzia mayottensis sp. nov.	Mayotte	Riv. Bouyouni	12°44'55"S, 45°08'36"E
		Riv. Coconi	12°50'05"S, 45°07'41"E
		Riv. Dembéni (lower course)	12°50'31"S, 45°10'22"E
		Riv. Dembéni (middle course)	12°51'07"S, 45°09'41"E
		Riv. Djalimou	12°57'14"S, 45°06'51"E
		Riv. Gouloué	12°47'27"S, 45°11'22"E
		Riv. Koualé (Loc. Légion)	12°48'00"S, 45°11'09"E
		Riv. Koualé (lower course)	12°48'20"S, 45°11'54"E
		Riv. Koualé (station 2)	12°47'49"S, 45°11'08"E
		Riv. Longoni	12°44'20"S, 45°09'53"E
		Riv. M'Tsangachéhi	12°53'04"S, 45°07'55"E
Labiobaetis glaucus	Anjouan	Riv. Ouani	12°09'30"S, 44°26'11"E
		Riv. Tatinga (lower course)	12°11'15"S, 44°29'52"E
	Mayotte	Riv. Bouyouni	12°44'55"S, 45°08'36"E
		Riv. Chirini, Soulou	12°46'40"S, 45°06'15"E
		Riv. Coconi	12°50'05"S, 45°07'41"E
		Riv. Coconi, Barakani	12°50'06"S, 45°07'44"E
		Riv. Dembéni (lower course)	12°50'31"S, 45°10'22"E
		Riv. Gouloué	12°47'27"S, 45°11'22"E
		Riv. Koualé (Loc. Légion)	12°48'00"S, 45°11'09"E
		Riv. Koualé (lower course)	12°48'20"S, 45°11'54"E
		Riv. Longoni	12°44'20"S, 45°09'53"E
		Riv. M'Tsangachéhi	12°53'04"S, 45°07'55"E
		Riv. Ourovéni	12°47'47"S, 45°08'22"E
Labiobaetis vinosus	Anjouan	Riv. Tatinga (lower course)	12°11'15"S, 44°29'52"E
Nigrobaetis richardi sp. nov.	Anjouan	Riv. Tatinga (lower course)	12°11'15"S, 44°29'52"E
		Riv. Tatinga (upper course)	12°12'34"S, 44°28'22"E
Potamocloeon (*A.*) *freitagae*	Anjouan	Riv. Santsa	12°17'31"S, 44°29'43"E
		Riv. Tatinga (upper course)	12°12'34"S, 44°28'22"E
Procloeon (*O.*) *cylindroculum*	Anjouan	Riv. Foumbani	12°11'40"S, 44°16'37"E
		Riv. Santsa	12°17'31"S, 44°29'43"E
	Mayotte	Riv. Longoni	12°44'20"S, 45°09'53"E

1. *Afroptilum bicorne* (Ulmer, 1909)

Figures 2a, 3–5

Diagnosis. Nymph. Following combination of characters: A) labrum on dorsal surface with a simple submedian seta, a submarginal arc of ca. six simple setae and one simple seta in between; B) both mandibles with stout setae between prostheca and mola; C) labial palp segment II with a poorly developed distomedial protuberance; segment III conical and slightly pointed, with a minute, pointed projection at inner basal margin; D) maxillary palp approximately as long as galea-lacinia; E) fore femur rather broad, length ca. 3× maximum width; dorsal margin with ca. 30 curved, spine-like setae; F) hind protoptera present; G) six pairs of gills.

Description. Nymph (Figs 2a, 3, 4). Body length 3.0–5.2 mm. Cerci: ca. 0.8× body length. Paracercus: ca. 2/3 of cerci length. Antenna: approx. 2× as long as head length.

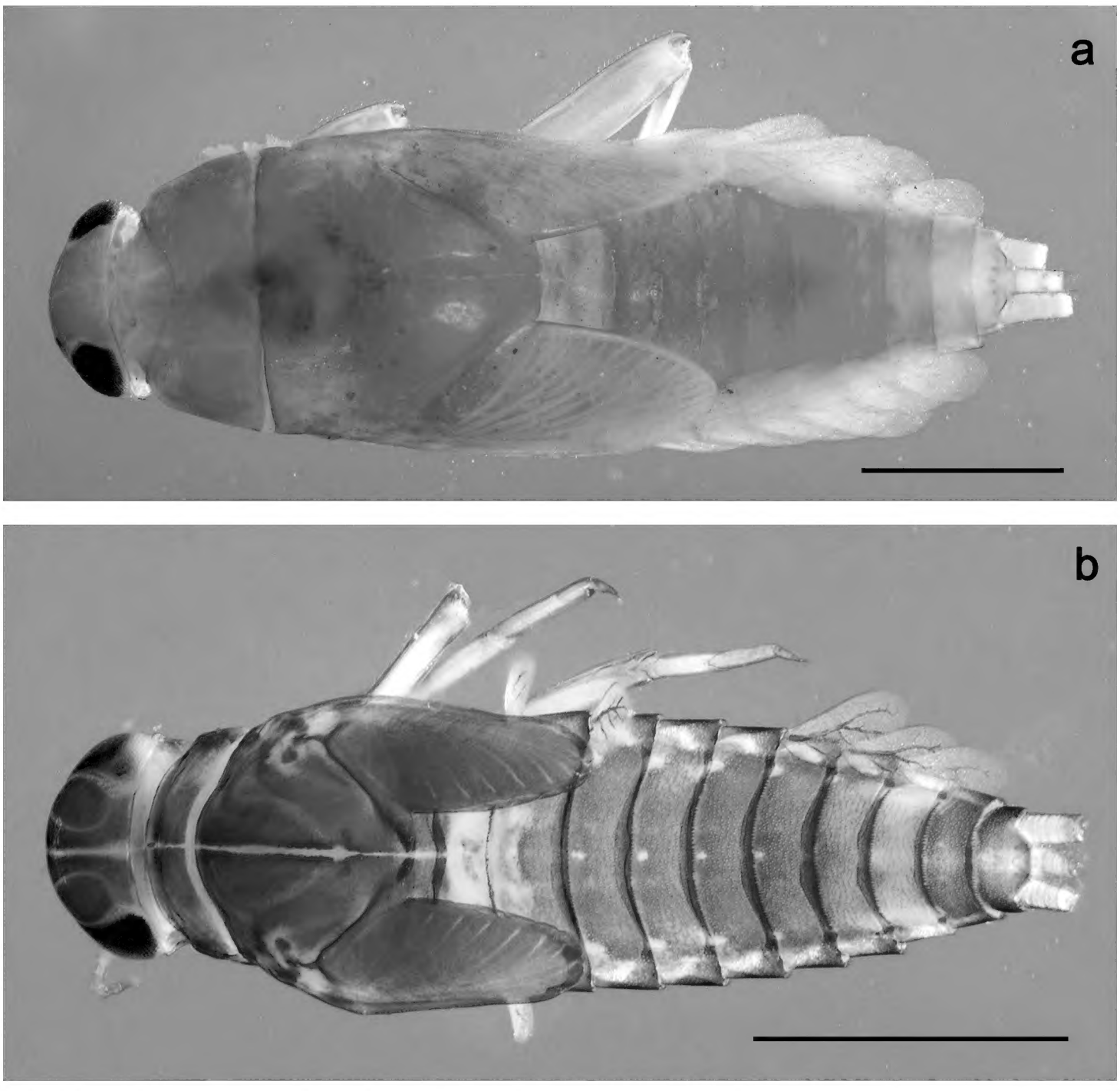


Figure 2. Nymphs, habitus: **a** *Afroptilum bicorne* **b** *Dabulamanzia mayottensis* sp. nov.

Colouration (Fig. 2a). Head, thorax and abdomen dorsally brown, abdominal segments II–VI medially with darker areas; head, thorax and abdomen ventrally light brown. Legs light brown, caudalii light brown.

Labrum (Fig. 3a). Subrectangular, length 0.7× maximum width. Distal margin with medial emargination and small process. Dorsally with long, fine, simple setae scattered over surface; a long, simple submedian seta, a submarginal arc of ca. six simple setae, decreasing in length laterally, and a medium, simple seta in between. Ventrally with marginal row of setae composed of lateral and anterolateral long, feathered setae and medial long, bifid setae; ventral surface with ca. six short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 3b, c). Incisor and kinetodontium partly fused. Incisor with five denticles; kinetodontium with three denticles. Prostheca stick-like, distolaterally laterally denticulate. Margin between prostheca and mola with many long, stout setae. Tuft of setae at apex of mola present.

Left mandible (Fig. 3d–f). Incisor and kinetodontium fused. Incisor with four denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with medium simple setae, and minute denticles towards subtriangular process. Subtriangular process long and slender, above level of area between prostheca and mola. Comb-shaped structure below subtriangular process. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlinguae (Fig. 3g). Lingua approximately as long as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed; distal half laterally not expanded. Superlinguae distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 3h). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, slightly directed against canines, middle and proximal denti-setae slender and pectinate. Medially with one spine-like seta and five or six simple setae, increasing in length distally. Maxillary palp approximately as long as length of galea-lacinia; 2-segmented; palp segment II 1.4× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment rounded.

Labium (Fig. 3i, j). Glossa basally broad, narrowing toward apex; slightly shorter than paraglossa; inner margin with eight spine-like setae; apex with one long and one medium, robust, pectinate setae; outer margin with five spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, curved inward; apex rounded; with three rows of long, robust setae in apical area, a row of long, robust setae on distolateral margin, and one short, simple seta in anteromedial area; dorsally with two long, spine-like, simple setae near inner margin. Labial palp with segment I 1.1× length of segments II and III combined. Segment I ventrally with short, fine, simple

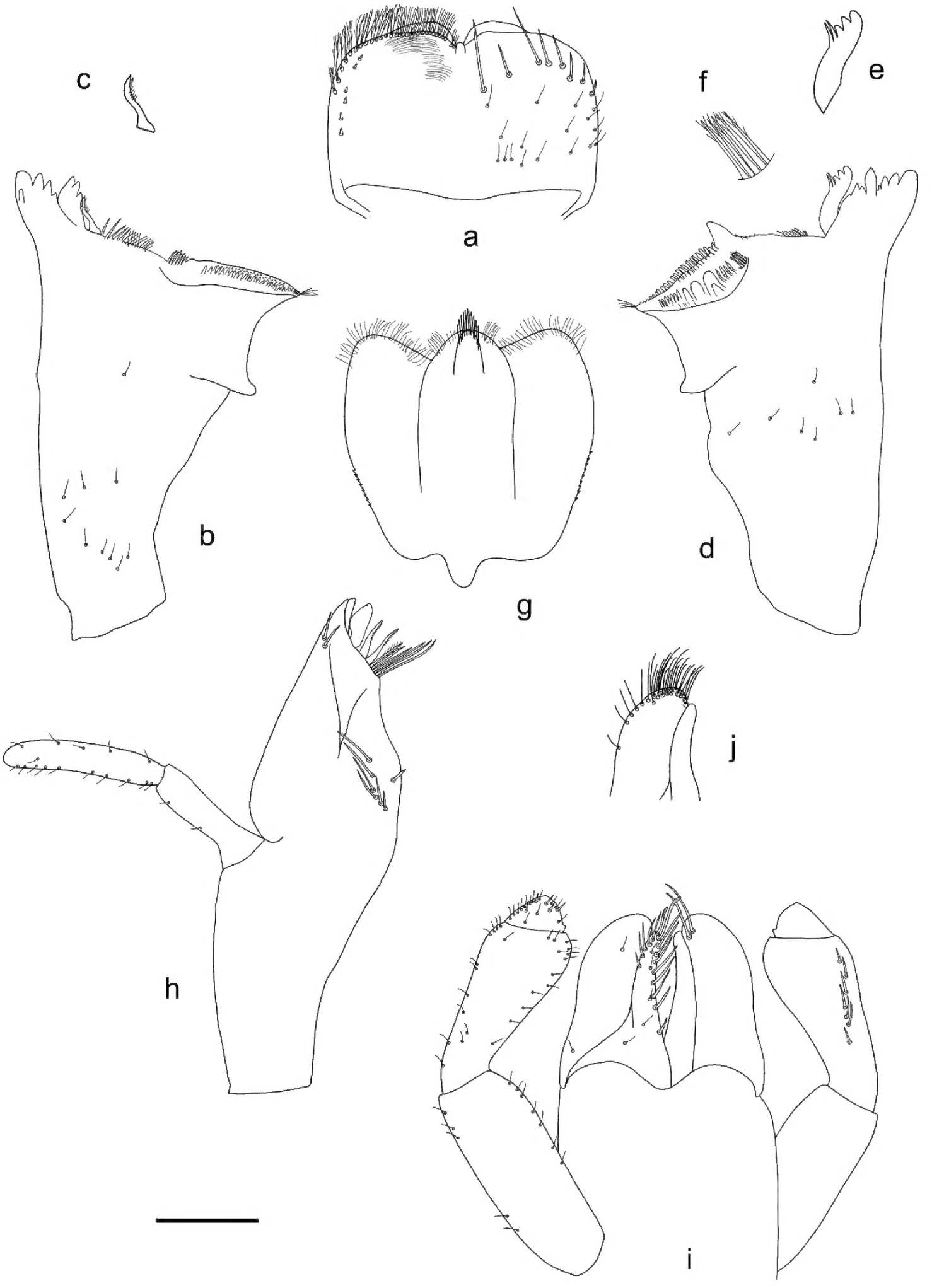


Figure 3. *Afroptilum bicorne*, nymph morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** comb-shaped structure below subtriangular process **g** hypopharynx and superlinguae **h** maxilla **i** labium **j** apex of paraglossa. Scale bar: 0.1 mm.

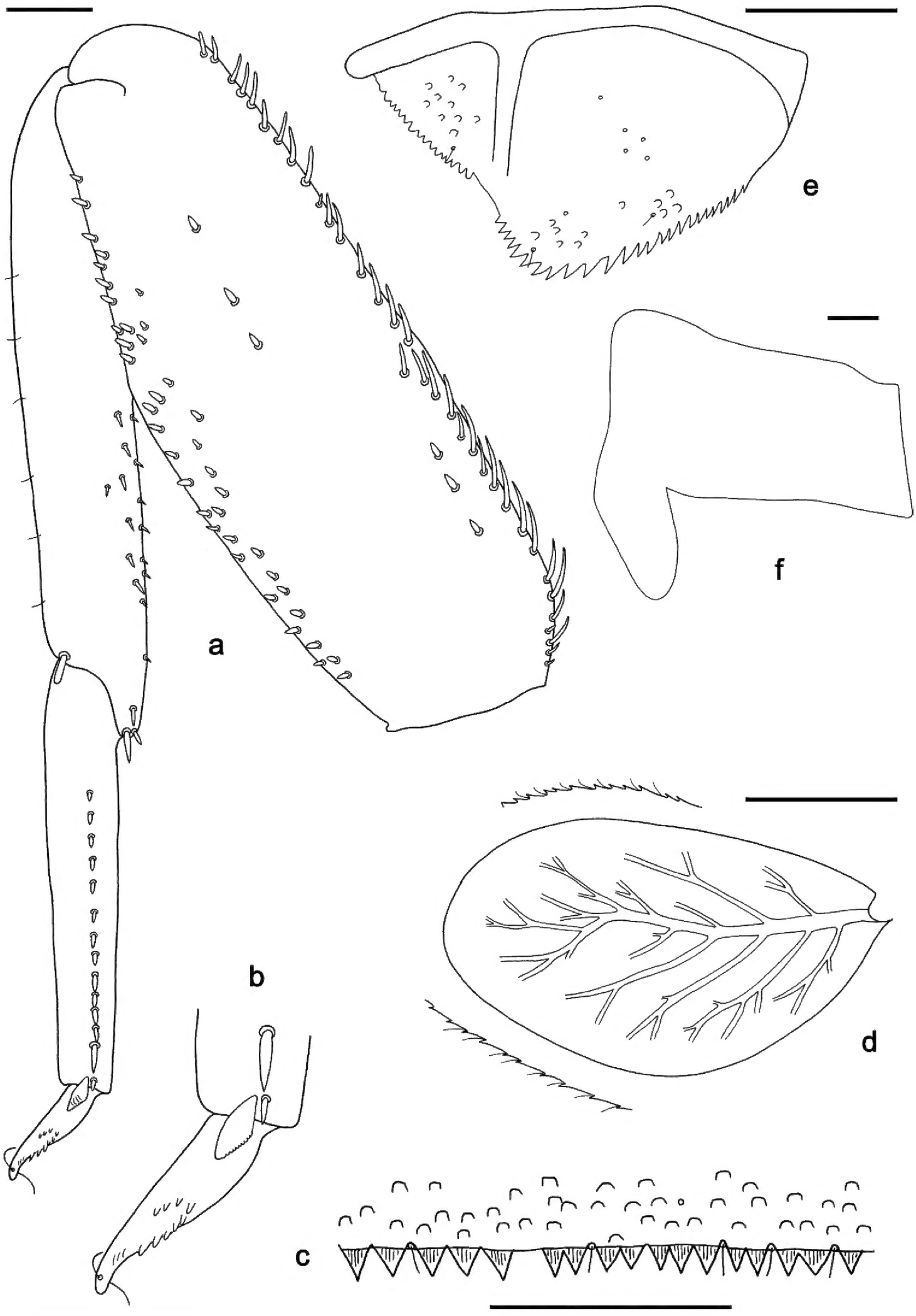


Figure 4. *Afroptilum bicorne*, nymph morphology: **a** foreleg **b** fore claw **c** tergum IV **d** gill IV **e** paraproct **f** metanotum (left side), with hind protopteron (mature nymph). Scale bars: 0.1 mm.

setae. Segment II with very slight distomedial protuberance; ventral surface with short, fine, simple setae; dorsally with 5–7 spine-like setae near outer margin. Segment III conical, apex slightly pointed; with a minute, pointed projection at inner basal margin; length 0.6× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 4f) well developed.

Foreleg (Fig. 4a, b). Ratio of foreleg segments 1.3:1.0:0.7:0.2. ***Femur.*** Length ca. 3× maximum width. Dorsal margin with 30 curved, spine-like setae. Apex rounded, with pair of spine-like setae. A few lanceolate setae scattered on distomedial surface. Short, stout, lanceolate setae scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with row of scarce, fine simple setae; on apex one stout, apically rounded seta. Ventral margin with row of short, curved, spine-like setae, on apex a few longer setae. Anterior surface scattered with short, stout, lanceolate setae. Patellotibial suture absent. ***Tarsus.*** Dorsal margin bare. Ventral margin with row of curved, spine-like setae. ***Claw*** with one row of six denticles and a second row of three denticles; distally pointed; with three or four stripes; one pair of long, subapical setae.

Middle and hind legs. As foreleg, but with patellotibial suture.

Terga (Fig. 4c). Surface with irregular rows of U-shaped scale bases. Posterior margin of tergum IV with triangular spines, approximately as long as wide.

Gills (Fig. 4d). Present on segments II–VII. Margin with small denticles intercalating short, fine, simple setae. Tracheae extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and VI combined; gill VII as long as length of segments VIII and IX combined.

Paraproct (Fig. 4e). Distally not expanded, with 25–35 marginal spines. Surface scattered with U-shaped scale bases and micropores. Cercotractor with small, marginal spines.

Description. Imago. See Ulmer 1909: p. 366, figs 1–3 and discussion below.

Distribution (Fig. 5). Comoros (Anjouan, Mohéli), Mayotte.

Biological aspects. In Mayotte, the specimens were collected at altitudes between sea level and 100 m, mostly together with one or several other species (*C. smaeleni*, *D. mayottensis* sp. nov., *L. glaucus*); in the Comoros, the specimens were collected at an altitude of 750 m, together with *P. freitagae* and *P. cylindroculum*. The characteristics and environmental conditions of the sampling site in the Comoros (Anjouan, Riv. Santsa) are described in Starmühlner (1979: p.651): river width 0.5–1 m, depth 2–10 cm, current 0.5– >1 m/s, water temperature ca. 24 °C, bottom substrata consisted of basaltic rock, boulders, gravel and sand at the borders.

Material examined. Comoros • 9 nymphs; Anjouan, Riv. Santsa, upper course, near Adda-Douéni; 750 m; 21.03.1974; leg. F. Starmühlner; 2 on slides; GBIFCH00592757, GBIFCH00592713; 7 in alcohol; GBIFCH00515654, GBIFCH00515708; MZL, FAMU. Mayotte • 1 nymph; Koualé, Affl. forêt 3; 12°47'43"S, 45°09'59"E; 18.05.2006; leg. N. Mary; on slide; GBIFCH00592758; MZL •

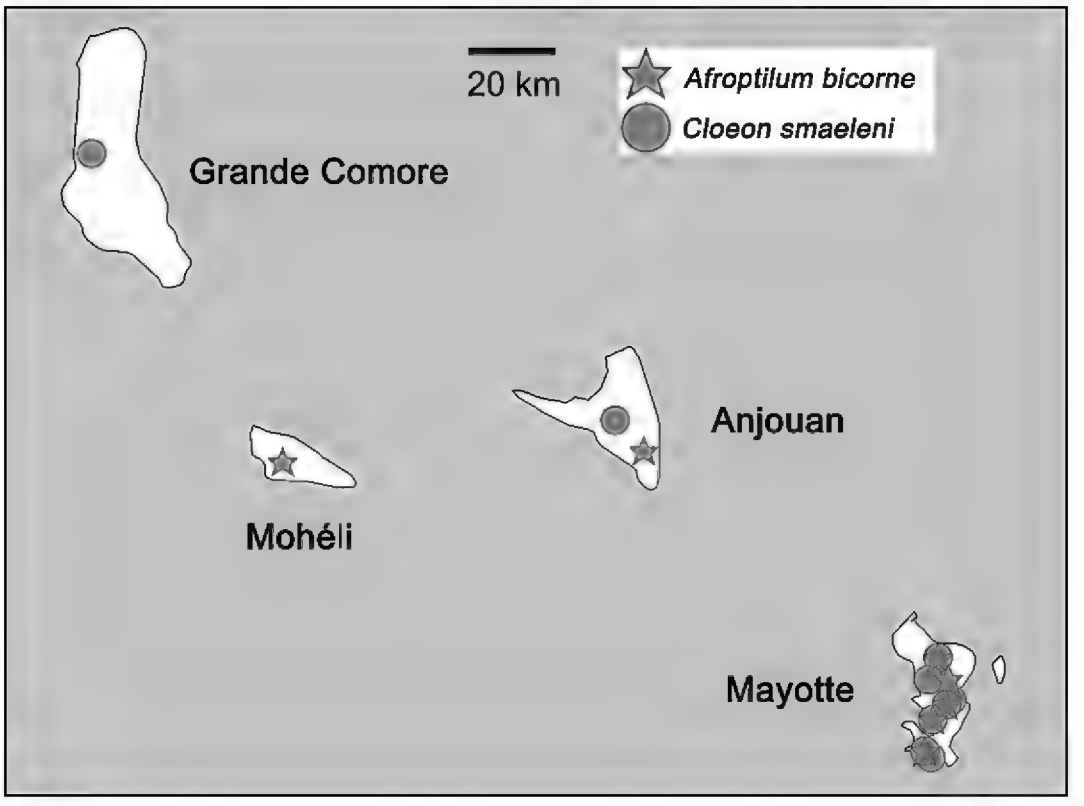


Figure 5. Distribution of *Afroptilum bicorne* and *Cloeon smaeleni* in the Comoros Archipelago.

78 nymphs; Bas. Riv. Djalimou, Djalimou aval; 12°57'14"S, 45°06'51"E; 15 m; 14.04.2009; leg. N. Mary; 2 on slides; GBIFCH00592714, GBIFCH00592722; 76 in alcohol; GBIFCH00515671, GBIFCH00515709; MZL, FAMU • 4 nymphs; Bas. M'Tsangachéhi, Loc. M'Tsangachéhi aval; 12°53'04"S, 45°07'55"E; 10 m; 14.04.2009; leg. N. Mary; in alcohol; GBIFCH00515674; MZL • 1 nymph; Bas. Riv. Bouyouni, Loc. Bouyouni intermédiaire; 12°44'55"S, 45°08'36"E; 40 m; 16.04.2009; leg. N. Mary; in alcohol; GBIFCH00515675; MZL • 15 nymphs; Riv. Dembéni, Loc. Dembéni intermédiaire; 12°51'07"S, 45°09'41"E; 95 m; 20.04.2009; leg. N. Mary; 1 on slide; GBIFCH00592723; 14 in alcohol; GBIFCH00515718; MZL.

2. *Cloeon smaeleni* Lestage, 1924

Cloeon smaeleni: Salles et al. 2014: figs 1–17; Gattolliat and Rabeantoandro 2002: figs 1–10.

Diagnoses. Nymph. Following combination of characters: A) labrum on dorsal surface with stout, simple setae in anterior part, not forming an arc; B) both mandibles with long, stout setae between prostheca and mola; C) labial palp with enlarged, falcate segment III; C) maxillary palp with three segments; D) claw with long pointed elongation; with two rows of denticles; E) gills formed by two lamellae, upper lamella rounded and almost as developed as the lower one.

Distribution (Fig. 5). Comoros (Grande Comore, Anjouan), Mayotte, La Réunion (Gattolliat 2004), Madagascar (Gattolliat and Rabeantoandro 2002), continental Afrotropics, Brazil (introduced, Salles et al. 2014 and citations therein).

Biological aspects. In the Comoros, the specimens were collected in a crater lake on the island of Anjouan at an altitude of 900 m and in a cistern with collected rainwater on Grande Comore (altitude 100 m). In Mayotte, the specimens were collected at altitudes from sea level to 100 m.

Material examined. Comoros • 66 nymphs; Anjouan, Lac Sacré, crater lake, slope of N'Tingiu Mtns; 900 m; 12.03.1974; leg. F. Starmühlner; 2 on slides; GBIFCH00592748, GBIFCH00592749; 64 in alcohol; GBIFCH00515661, GBIFCH00515662, GBIFCH00515663; MZL, FAMU • 17 nymphs; Grande Comore, in village N of Moroni; 28.02.1974; leg. F. Starmühlner; in alcohol; GBIFCH00515664; MZL, FAMU. Mayotte • 1 nymph; Riv. Dembéni, Loc. Dembéni aval; 12°50'31"S, 45°10'22"E; 10 m; 17.05.2006; leg. N. Mary; on slide; GBIFCH00592751; MZL • 1 nymph; Bas. Ourovéni, Riv. Haoutoungou, Lac Karihani; 12°47'49"S, 45°07'20"E; 19.05.2006; leg. N. Mary; on slide; GBIFCH00592752; MZL • 3 nymphs; Bas. Riv. Djalimou, Djalimou aval; 12°57'14"S, 45°06'51"E; 15 m; 14.04.2009; leg. N. Mary; in alcohol; GBIFCH00515672; FAMU • 1 nymph; Bas. M'Tsangachéhi, Loc. M'Tsangachéhi aval; 12°53'04"S, 45°07'55"E; 10 m; 14.04.2009; leg. N. Mary; in alcohol; GBIFCH00515676; MZL • 1 nymph; Bas. Riv. Bouyouni, Loc. Bouyouni intermédiaire; 12°44'55"S, 45°08'36"E; 40 m; 16.04.2009; leg. N. Mary; in alcohol; GBIFCH00515678; MZL • 2 nymphs; Riv. Dembéni, Loc. Dembéni intermédiaire; 12°51'07"S, 45°09'41"E; 95 m; 20.04.2009; leg. N. Mary; in alcohol; GBIFCH00515717; MZL • 1 nymph; Riv. Dapani aval, P1; 12°58'05"S, 45°07'39"E; 25 m; 19.08.2018; leg. N. Mary; in alcohol; MZL.

3. *Dabulamanzia mayottensis* sp. nov.

http://zoobank.org/D1C96541-329C-44B3-BB6E-AAE1EA5C500B
Figures 2b, 6–8

Diagnosis. Nymph. Following combination of characters: A) labrum on dorsal surface with a simple submedian seta and a submarginal arc of four simple setae; B) both mandibles with stout setae between prostheca and mola; C) labium with glossae as long as paraglossae, labial palp segment II without protuberance; C) maxillary palp slightly longer than galea-lacinia, segment II apically pointed; D) fore femur rather broad, length ca. 3× maximum width; dorsal margin with ca. 12 curved, spine-like setae; tibia proximally with long arc of long, simple setae; E) hind protoptera well developed; F) seven pairs of gills.

Description. Nymph (Figs 2b, 6, 7). Body length 3.0–4.0 mm. Cerci: ca. 2/3 of body length. Paracercus: slightly shorter than cerci. Antenna: approx. 2× as long as head length.

Colouration (Fig. 2b). Head, thorax and abdomen dorsally brown, with pattern as in Fig. 2b. Head, thorax and abdomen ventrally light brown. Legs mainly light brown, femur with dorsomedial brown streak, apex brown; tibia proximally brown; tarsus brown. Caudalii light brown.

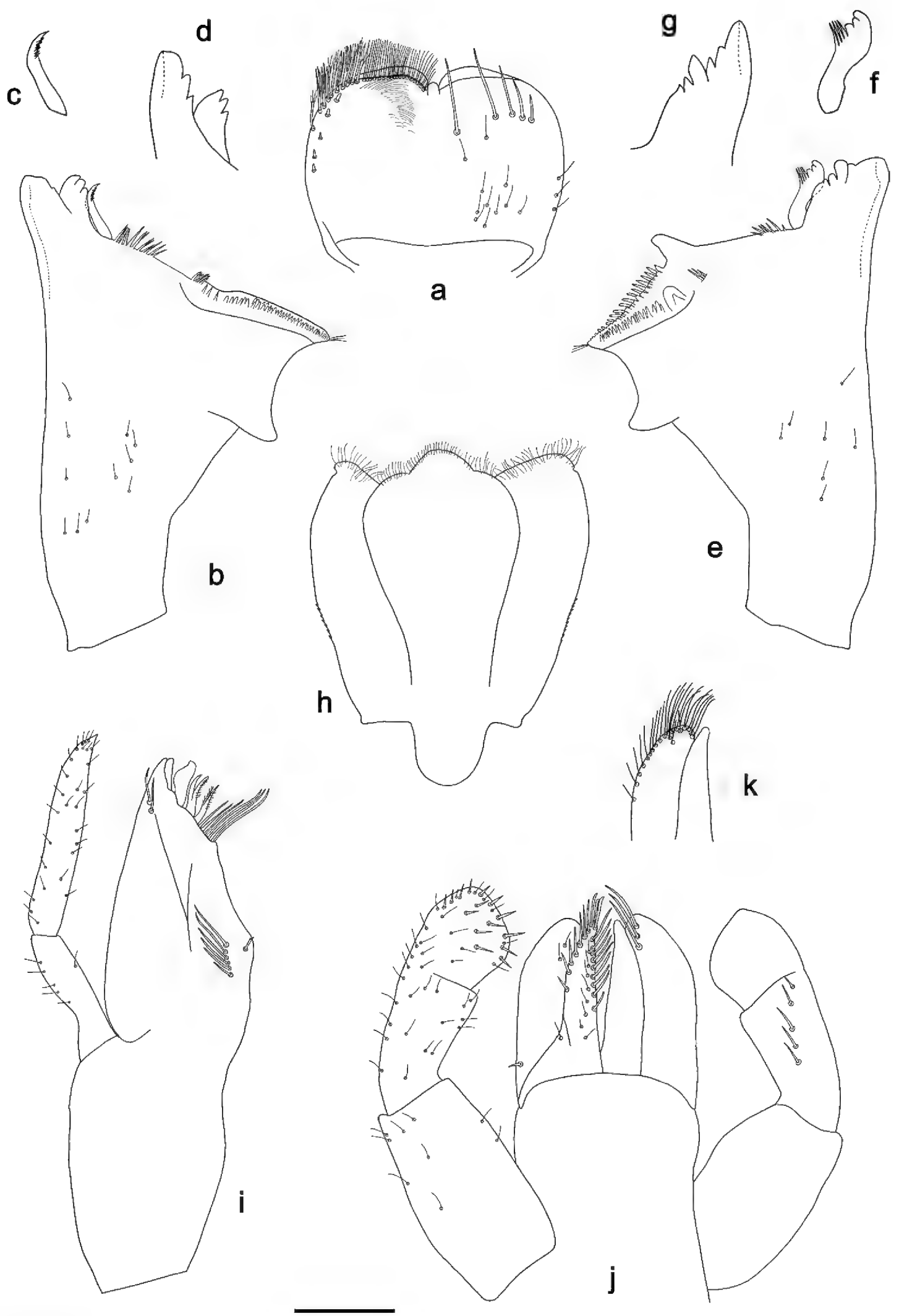


Figure 6. *Dabulamanzia mayottensis* sp. nov., nymph morphology: **a** labrum **b** right mandible **c** right prostheca **d** right incisor and kinetodontium **e** left mandible **f** left prostheca **g** Left incisor and kinetodontium **h** hypopharynx and superlinguae **i** maxilla **j** labium **k** apex of paraglossa. Scale bar: 0.1 mm.

Labrum (Fig. 6a). Subrectangular, length 0.7× maximum width. Distal margin with medial emargination and small process. Dorsally with long, fine, simple setae scattered over surface; one simple submedian seta and submarginal arc of four simple setae. Ventrally with marginal row of setae composed anterolateral long, feathered setae and medial long, bifid setae; ventral surface with ca. five short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 6b–d). Incisor and kinetodontium partly fused. Incisor with three denticles, distal denticle blade-like; kinetodontium with three denticles. Prostheca stick-like, distolaterally denticulate. Margin between prostheca and mola straight, with long, stout setae. Tuft of setae at apex of mola present.

Left mandible (Fig. 6e–g). Incisor and kinetodontium fused. Incisor with three denticles, distal denticle blade-like; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with medium, stout setae. Subtriangular process long and slender, above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlinguae (Fig. 6h). Lingua as long as superlinguae. Lingua longer than broad; distal half laterally slightly expanded; distal margin with short, fine setae, tuft of stout setae absent. Superlinguae distally straight; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 6i). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like and slightly directed against canines; middle and proximal denti-setae slender, bifid and pectinate. Medially with one pectinate, spine-like seta and five or six long, simple setae. Maxillary palp slightly longer than length of galea-lacinia; 2-segmented; palp segment II 1.7× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment pointed.

Labium (Fig. 6j, k). Glossa basally broad, narrowing toward apex; as long as paraglossa; inner margin with nine spine-like setae, increasing in length distally; apex with three long, robust setae; outer margin with seven or eight spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, curved inward; apex rounded; with many long, robust setae in apical area and along apicolateral margin; two short, simple setae in anteromedial area; dorsally with row of three long, spine-like, simple setae near inner margin. Labial palp with segment I 0.9× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II without distomedial protuberance; ventral surface with short, fine, simple setae; dorsally with five spine-like setae. Segment III slightly pentagonal; length 1.1× maximum width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 7f) well developed.

Foreleg (Fig. 7a, b). Ratio of foreleg segments 1.8:1.0:1.0:0.3. ***Femur.*** Length ca. 3× maximum width. Dorsal margin with 9–12 curved, spine-like setae. Apex rounded, with pair of spine-like setae and fine, simple setae. Stout, lanceolate setae

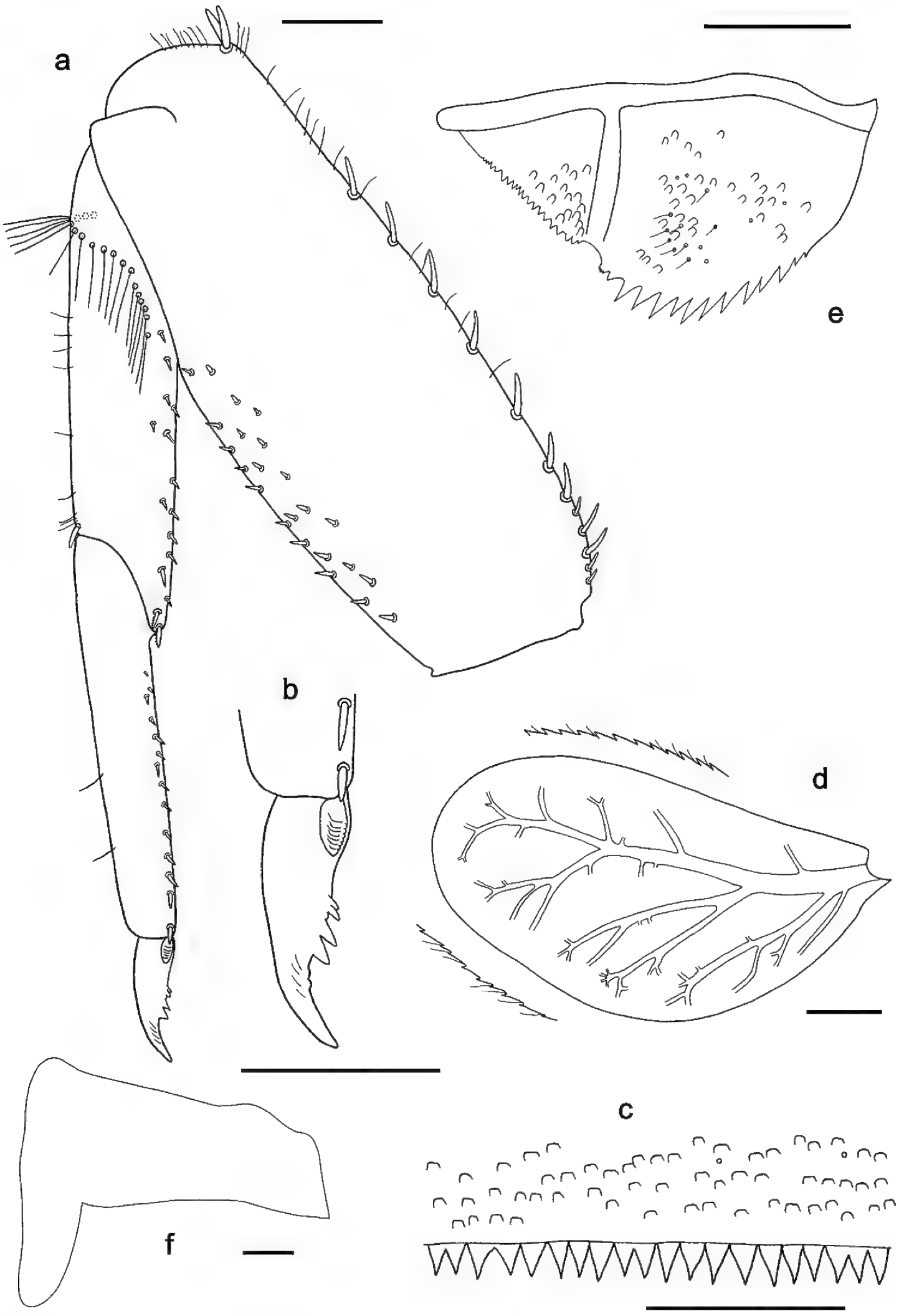


Figure 7. *Dabulamanzia mayottensis* sp. nov., nymph morphology: **a** foreleg **b** fore claw **c** tergum IV **d** gill IV **e** paraproct **f** metanotum (left side), with hind protopteron (mature nymph). Scale bars: 0.1 mm.

scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with row of fine simple setae. Ventral margin with row of short, curved, spine-like setae, on apex some longer, pectinate setae. Anterior surface scattered with few short, stout, lanceolate setae; proximally long arc of long, fine, simple setae, reaching posterior side. Patellotibial suture absent. ***Tarsus.*** Dorsal margin almost bare. Ventral margin with row of short, curved, spine-like setae. ***Claw*** with one row of four denticles, the two distal ones larger than the two proximal ones; distally pointed; with ca. four stripes; subapical setae absent.

Middle and hind legs. As foreleg, but with patellotibial suture.

Terga (Fig. 7c). Surface with irregular rows of U-shaped scale bases and scattered micropores. Posterior margin of tergum IV with triangular spines, longer than wide.

Gills (Fig. 7d). Present on segments I–VII. Margin with small denticles intercalating short, fine, simple setae. Tracheae extending from main trunk to inner and outer margins. Gill I as long as ¾ length of segment II, gill IV as long as length of segments V and VI combined; gill VII as long as length of segments VIII and IX combined.

Paraproct (Fig. 7e). Distally not expanded, with 14–16 marginal spines. Surface scattered with U-shaped scale bases, fine, simple setae and micropores. Cercotractor with small, marginal spines.

Etymology. With reference to the island of Mayotte, where the type locality is.

Distribution (Fig. 8). Mayotte.

Biological aspects. The specimens were collected at altitudes between sea level and 110 m, mostly together with one or several other Baetidae species living in Mayotte (*Afroptilum bicorne*, *Cloeon smaeleni*, *Labiobaetis glaucus*, *Procloeon cylindroculum*).

Type material. ***Holotype.*** Mayotte • nymph; Riv. Dembéni, Loc. Dembéni intermédiaire; 12°51'07"S, 45°09'41"E; 95 m; 20.04.2009; leg. N. Mary; on slide; GBIFCH00592797; MZL. ***Paratypes.*** Mayotte • 11 nymphs; same data as holotype; in alcohol; GBIFCH00515706, GBIFCH00515719; MZL, FAMU • 2 nymphs; Riv. Longoni, Loc. Longoni aval; 12°44'20"S, 45°09'53"E; 30 m; 14.05.2006; leg. N. Mary; on slides; GBIFCH00592746, GBIFCH592747; MZL • 25 nymphs; Riv. Longoni, Loc. Longoni aval; 12°44'20"S, 45°09'53"E; 30 m; 16.04.2009; leg. N. Mary; 2 on slides; GBIFCH00592720, GBIFCH00592721; 23 in alcohol; GBIFCH00515703, GBIFCH00515724; MZL, FAMU • 2 nymphs; Riv. Dembéni, Loc. Dembéni aval; 12°50'31"S, 45°10'22"E; 10 m; 17.05.2006; leg. N. Mary; on slide; GBIFCH00592760; MZL • 20 nymphs; Riv. Dembéni, Loc. Dembéni aval; 12°50'31"S, 45°10'22"E; 10 m; 19.04.2009; leg. N. Mary; in alcohol; GBIFCH00515723; MZL • 13 nymphs; Bas. Riv. Djalimou, Djalimou aval; 12°57'14"S, 45°06'51"E; 15 m; 14.04.2009; leg. N. Mary; in alcohol; GBIFCH00515673; MZL • 5 nymphs; Bas. M'Tsangachéhi, Loc. M'Tsangachéhi aval; 12°53'04"S, 45°07'55"E; 10 m; 14.04.2009; leg. N. Mary; in alcohol; GBIFCH00515677; MZL • 44 nymphs; Bas. Riv. Bouyouni, Loc. Bouyouni intermédiaire; 12°44'55"S, 45°08'36"E; 40 m; 16.04.2009; leg. N. Mary; in alcohol; GBIFCH00515679, GBIFCH00515680; MZL • 53 nymphs; Riv. Koualé, Loc. Légion; 12°47'49"S, 45°11'08"E; 50 m; 21.04.2009;

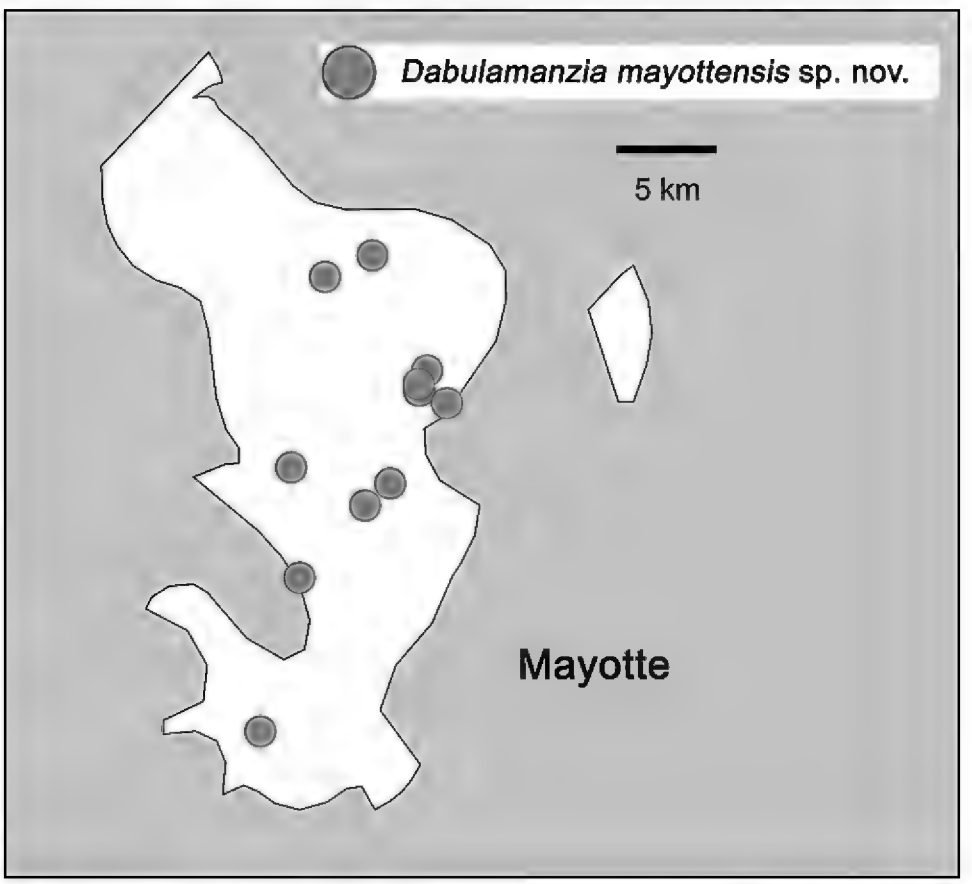


Figure 8. Distribution of *Dabulamanzia mayottensis* sp. nov. in Mayotte.

leg. N. Mary; in alcohol; GBIFCH00515722; MZL • 20 nymphs; Riv. Koualé, Loc. Koualé aval; 12°48'20"S, 45°11'54"E; 10 m; 13.04.2009; leg. N. Mary; in alcohol; GBIFCH00515721; MZL • 1 nymph; Riv. Koualé, Loc. Koualé, st. 2; 12°48'00"S, 45°11'09"E; 50 m; 17.05.2006; leg. N. Mary; in alcohol; GBIFCH00515704; MZL • 20 nymphs; Bas. Riv. Gouloué, Loc. Gouloué captage; 12°47'27"S, 45°11'22"E; 110 m; 15.04.2009; leg. N. Mary; in alcohol; GBIFCH00515720; MZL • 2 nymphs; Bas. Riv. Coconi, Loc. Coconi aval cascade; 12°50'05"S, 45°07'41"E; 02.2018; leg. N. Mary; in alcohol; GBIFCH00515705; MZL.

4. *Labiobaetis glaucus* (Agnew, 1961)

Labiobaetis glaucus: Agnew 1961 (*Baetis glaucus*); Lugo-Ortiz and McCafferty 1997: figs 27–38, 39–50 (*Labiobaetis masai*, *L. nadineae*; formal synonyms, Lugo-Ortiz et al. 2000); Lugo-Ortiz et al. 2000: figs 1–11 (*Pseudocloeon glaucum*); Gattolliat et al. 2018: figs 34–44, 47.

Diagnosis. Nymph. Following combination of characters: A) labrum on dorsal surface with submarginal arc of feathered setae; B) labial palp segment II with broad thumb-like protuberance; C) maxillary palp segment II with excavation at inner distolateral margin; D) fore femur rather broad, length 3× maximum width; dorsal margin with 13–18 curved, spine-like setae and often basally some additional setae

near margin; femoral patch well developed; E) hind protoptera well developed; F) seven pairs of gills.

Distribution (Fig. 9). Angola, Comoros, Ethiopia, Guinea, potentially Iran, Ivory Coast, Kenya, Lesotho, Mali, Mayotte, Namibia, Saudi Arabia, South Africa, Zimbabwe (Kaltenbach and Gattolliat 2021 and citations therein).

Biological aspects. In the Comoros, the specimens were collected at an altitude of approximately 200 m, together with *L. vinosus* and *N. richardi* sp. nov. The characteristics and environmental conditions of the sampling sites in the Comoros (Anjouan, Riv. Tatinga, Riv. Ouani) are described in Starmühlner (1979: pp. 654, 655): river width 4–10 m, depth 5–30 cm, water temperature ca. 25 °C, bottom substrata consisted of basaltic boulder, gravel and muddy sand. In Mayotte, the specimens were collected at altitudes from sea level to 80 m, partly together with *A. bicorne*, *C. smaeleni*, *D. mayottensis* sp. nov. and *P. cylindroculum*.

Material examined. Comoros • 9 nymphs; Anjouan, Riv. Tatinga, lower course by the bridge; 210 m; 22.03.1974; leg. F. Starmühlner; 1 on slide; GBFCH00592742; 8 in alcohol; GBIFCH00515668, GBIFCH00515670; MZL, FAMU • 163 nymphs; Anjouan, Ouani Riv., upper course by a tributary; 250 m; 08.03.1974; leg. F. Starmühlner; 2 on slides; GBIFCH00592743, GBIFCH00592744; 161 in alcohol; GBIFCH00515666, GBIFCH00515667, GBIFCH00515669; MZL, FAMU. Mayotte • 51 nymphs; Riv. Ourovéni; 12°47'47"S, 45°08'22"E; 80 m; 30.08.2013; leg. N. Mary; in alcohol; GenBank MH070318, GBIFCH00515530, GBIFCH00515688; MZL, FAMU • 30 nymphs, Riv. Ourovéni; 12°47'47"S, 45°08'22"E; 80 m; 19.05.2006; leg. N. Mary; in alcohol; GBIFCH00515689; MZL, FAMU • 1 nymph; Mayotte; Coconi; 29.08.2013; leg. N. Mary; 1 in alcohol; GenBank MH105069; GBIFCH00515531; MZL • 37 nymphs; Bas. Riv. Coconi, Loc. Coconi aval cascade; 12°50'05"S, 45°07'41"E; 17.04.2009; leg. N. Mary; in alcohol; GBIFCH00515712, GBIFCH00515714; MZL • 41 nymphs; Riv. Longoni, Loc. Longoni aval; 12°44'20"S, 45°09'53"E; 30 m; 16.04.2009; leg. N. Mary; in alcohol; GBIFCH00515711, GBIFCH00515713; MZL • 18 nymphs; Riv. Koualé, Loc. Légion; 12°47'49"S, 45°11'08"E; 50 m; 21.04.2009; leg. N. Mary; in alcohol; GBIFCH00515710; MZL • 50 nymphs; Riv. Koualé, Loc. Koualé aval; 12°48'20"S, 45°11'54"E; 10 m; 17.05.2006; leg. N. Mary; in alcohol; GBIFCH00515691; MZL • 7 nymphs; Riv. M'Tsangachéhi; 12°53'04"S, 45°07'55"E; 10 m; 16.05.2006; leg. N. Mary; in alcohol; GBIFCH00515693; MZL • 70 nymphs; Bas. Coconi, Riv. Coconi, Barakani; 12°50'06"S, 45°07'44"E; 19.05.2006; leg. N. Mary; in alcohol; GBIFCH00515692; MZL • 1 nymph; Bas. Riv. Bouyouni, Loc. Bouyouni intermédiaire; 12°44'55"S, 45°08'36"E; 40 m; 15.05.2006; leg. N. Mary; in alcohol; GBIFCH00515690; MZL • 4 nymphs; Bas. Chirini, Riv. Chirini, Soulou; 12°46'40"S, 45°06'15"E; 16.05.2006; leg. N. Mary; in alcohol; GBIFCH00515687; MZL • 20 nymphs; Riv. Dembéni, Loc. Dembéni aval; 12°50'31"S, 45°10'22"E; 10 m; 19.04.2009; leg. N. Mary; in alcohol; GBIFCH00515716; MZL • 15 nymphs; Bas. Riv. Gouloué, Loc. Gouloué captage; 12°47'27"S, 45°11'22"E; 110 m; 15.04.2009; leg. N. Mary; in alcohol; GBIFCH00515715; MZL.

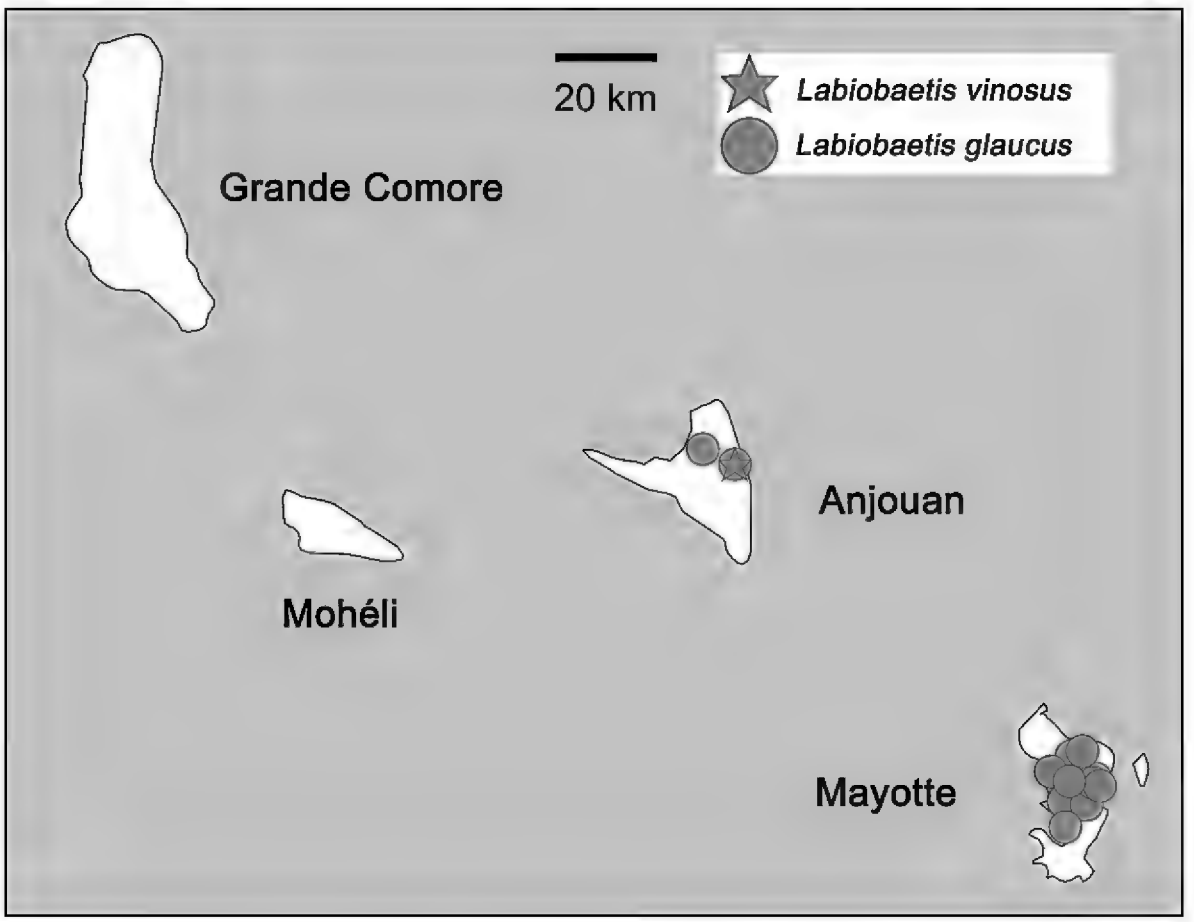


Figure 9. Distribution of *Labiobaetis glaucus* and *Labiobaetis vinosus* in the Comoros Archipelago.

5. *Labiobaetis vinosus* (Barnard, 1932)

Labiobaetis vinosus: Barnard 1932 (*Baetis vinosus*); Gillies 1994: figs 16–26 (*Baetis spatulatus*; formal synonym, Kluge and Novikova 2016); Lugo-Ortiz and McCafferty 1997: figs 75–86; Kluge and Novikova 2016: figs 113, 122–129, 132, 133 (*L. tenuicrinitus*; informal synonym, Kluge 2021).

Diagnosis. Nymph. Following combination of characters: A) labrum on dorsal surface with submarginal arc of feathered setae; B) labial palp segment II with broad, thumb-like protuberance; C) maxillary palp segment II with excavation at inner distolateral margin; D) fore femur rather broad, length ca. 3× maximum width; dorsal margin with 8–18 curved, spine-like setae and basally a partial second row of setae; E) hind protoptera absent or minute; F) six pairs of gills.

Distribution (Fig. 9). Angola, Comoros, DR Congo, Ethiopia, Ivory Coast, South Africa, Tanzania, Uganda (Kaltenbach and Gattolliat 2021 and citations therein).

Biological aspects. The specimens were collected at an altitude of 210 m, together with *L. glaucus* and *N. richardi* sp. nov. The characteristics and environmental conditions of the sampling site (Anjouan, Riv. Tatinga) are described in Starmühlner (1979: p. 654): river width 4–8 m, depth 5–10 cm, water temperature ca. 25 °C, bottom substrata consisted of basaltic boulder, gravel and muddy sand.

Material examined. Comoros • 3 nymphs; Anjouan, Riv. Tatinga, lower course by the bridge; 210 m; 22.03.1974; leg. F. Starmühlner; 2 on slides; GBIFCH00592719, GBIFCH00592745; 1 in alcohol; GBIFCH00515665; MZL.

6. *Nigrobaetis richardi* sp. nov.

http://zoobank.org/F86BB1BA-E1C9-4C37-8404-8E1EBEFD9407
Figures 10a, 11–13

Diagnosis. Nymph. Following combination of characters: A) labrum on dorsal surface with ca. six stout, simple setae in distal half; B) right mandible with medium, stout setae between prostheca and mola; left mandible with minute denticles between prostheca and mola; C) labial palp segment II without distomedial protuberance; segment III slightly pentagonal; D) fore femur rather broad, length ca. 3× maximum width; dorsal margin with 8–10 curved, lanceolate setae, apically pointed ; femoral patch absent; E) hind protoptera well developed; F) seven pairs of gills; G) paraproct with 5–7 marginal spines.

Description. Nymph (Figs 10a, 11, 12). Body length 3.3–3.8 mm. Cerci: broken. Paracercus: ca. ½ of body length. Antenna: broken.

Colouration (Fig. 10a). Head, thorax and abdomen dorsally brown, tergites I, IV, VIII and IX light brown, ventrally light brown. Legs light brown, caudalii light brown.

Labrum (Fig. 11a). Subrectangular, length 0.7× maximum width. Distal margin with medial emargination and small process. Dorsally in proximal half with long, fine, simple setae scattered over surface; in distal half with one central, long, stout, simple seta, two longer and some shorter stout, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae; ventral surface with ca. five short, spine-like setae near lateral and anterolateral margin.

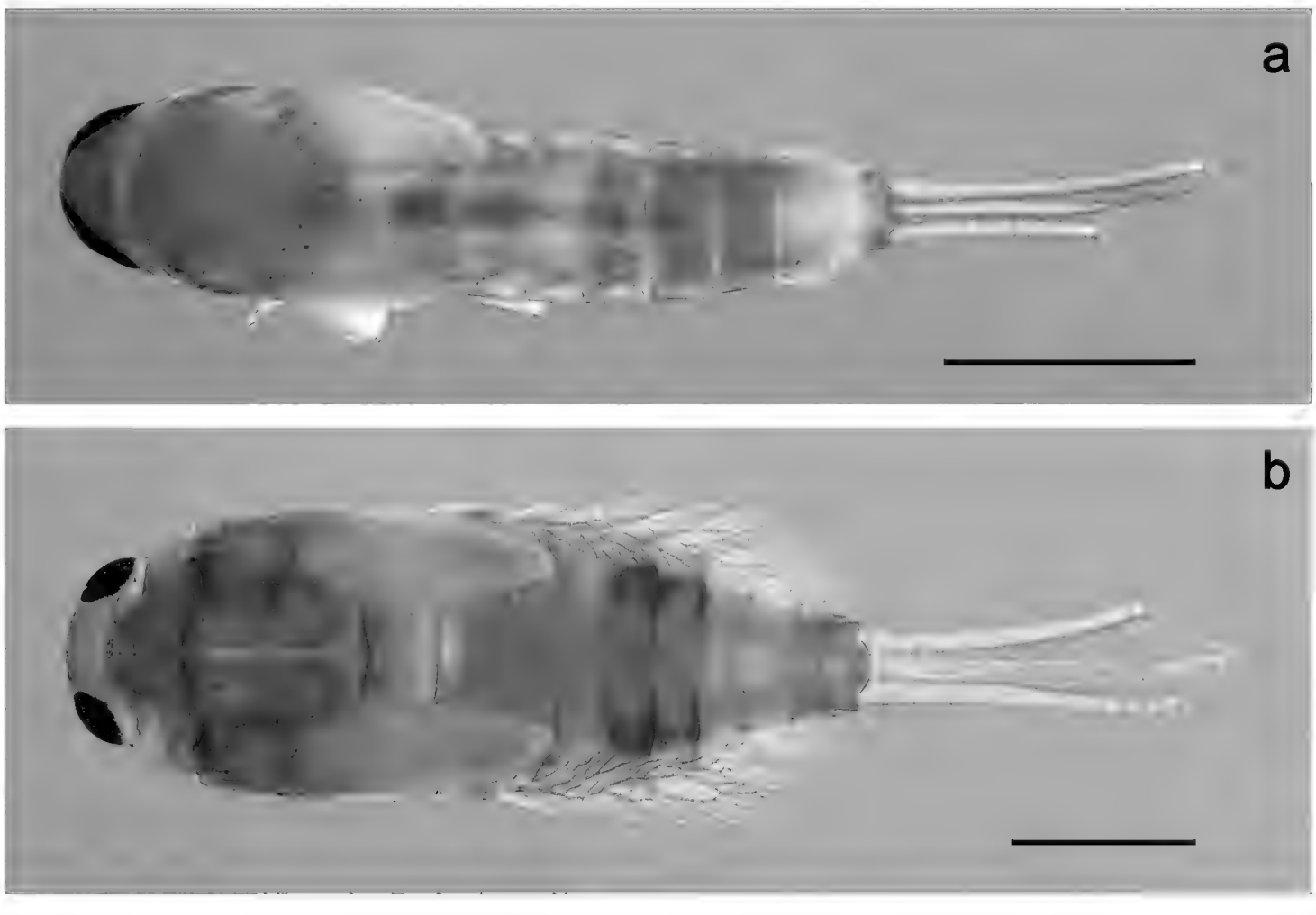


Figure 10. Nymphs, habitus: **a** *Nigrobaetis richardi* sp. nov. **b** *Potamocloeon* (*A.*) *freitagae*.

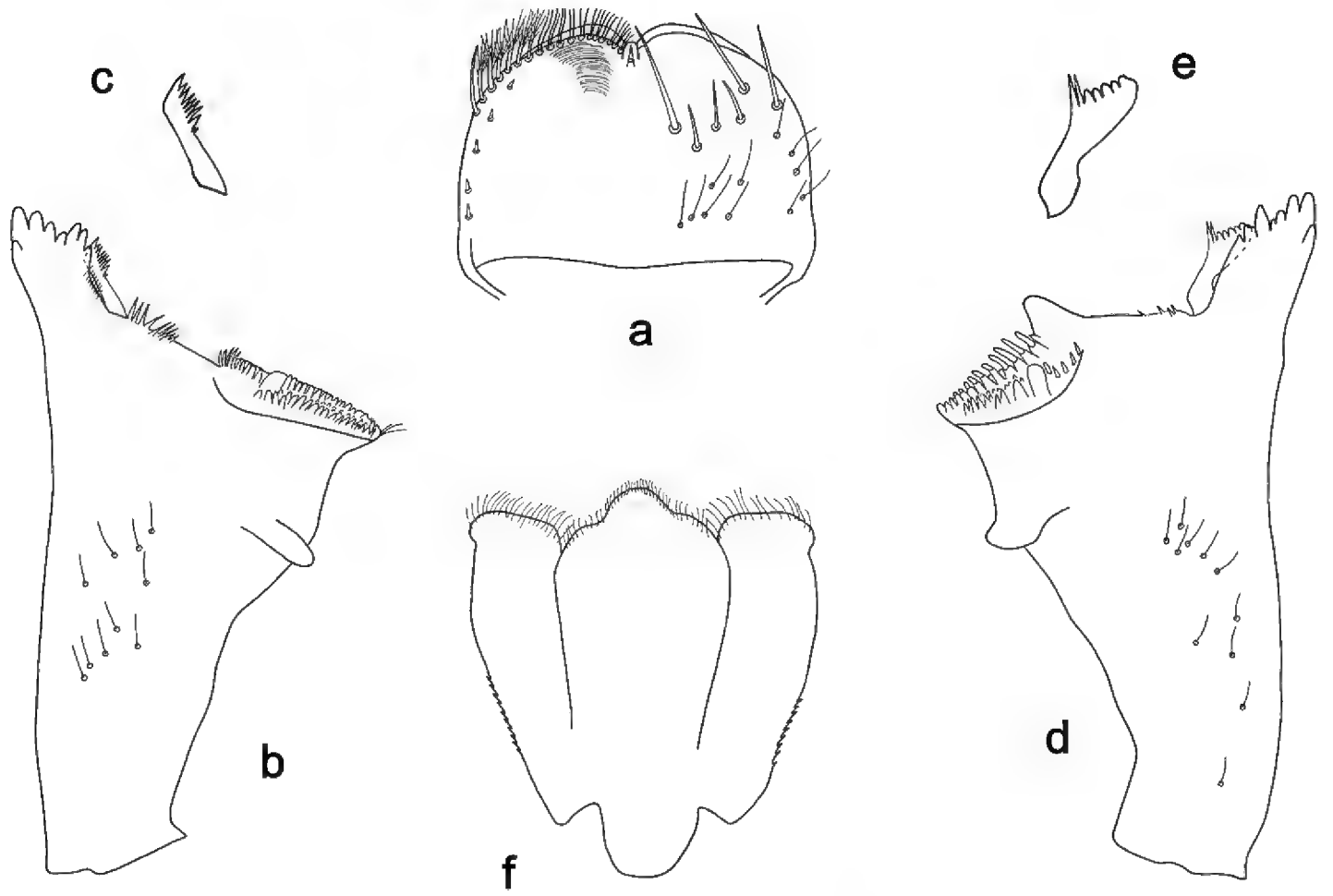


Figure 11. *Nigrobaetis richardi* sp. nov., nymph morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** hypopharynx and superlinguae **g** maxilla **h** labium **i** apex of paraglossa. Scale bar: 0.1 mm.

Right mandible (Fig. 11b, c). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles, inner margin of innermost denticle with row of thin setae. Prostheca stick-like, distolaterally denticulate. Margin between prostheca and mola straight, with medium, stout setae. Tuft of setae at apex of mola present.

Left mandible (Fig. 11d, e). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with minute denticles. Subtriangular process long and slender, above level of area between prostheca and mola. Tuft of setae at apex of mola absent.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlinguae (Fig. 11f). Lingua slightly longer than superlinguae. Lingua longer than broad; medial tuft of stout setae absent; distal half laterally slightly expanded. Superlinguae distally straight; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 11g). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one spine-like seta and four long, simple setae. Maxillary palp longer than length of galea-lacinia; 2-segmented; palp segment II 1.2× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment slightly pointed.

Labium (Fig. 11h, i). Glossa basally broad, narrowing toward apex; as long as paraglossa; inner margin with seven spine-like setae; apex with two long, robust setae and one short, robust, pectinate seta; outer margin with six spine-like setae. Paraglossa sub-rectangular, curved inward; apex rounded; with three rows of long, robust setae in apical area, two short, simple setae in anteromedial area and one short, simple seta in posterolateral area; dorsally with row of three long, spine-like, simple setae near inner margin. Labial palp with segment I approximately as long as length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II without distomedial protuberance; ventral surface with short, fine, simple setae; dorsally with four spine-like setae. Segment III slightly pentagonal; length 1.1× maximum width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 12g) well developed.

Foreleg (Fig. 12a–c). Ratio of foreleg segments 1.3:1.0:0.6:0.2. ***Femur.*** Length ca. 3× maximum width. Dorsal margin with 8–10 curved, lanceolate setae, apically pointed. Apex rounded, with pair of spine-like setae and fine, simple setae. Stout, lanceolate setae scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with row of scarce, fine simple setae. Ventral margin with row of scarce, short, curved, spine-like setae, on apex some longer, partly pectinate setae. Anterior surface scattered with short, stout, lanceolate setae. Patellotibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with row of scarce, fine, simple setae. Ventral margin with row of curved, spine-like setae, partly pectinate. ***Claw*** with one row of 12 or 13 denticles; distally pointed; with ca. three stripes; subapical setae absent.

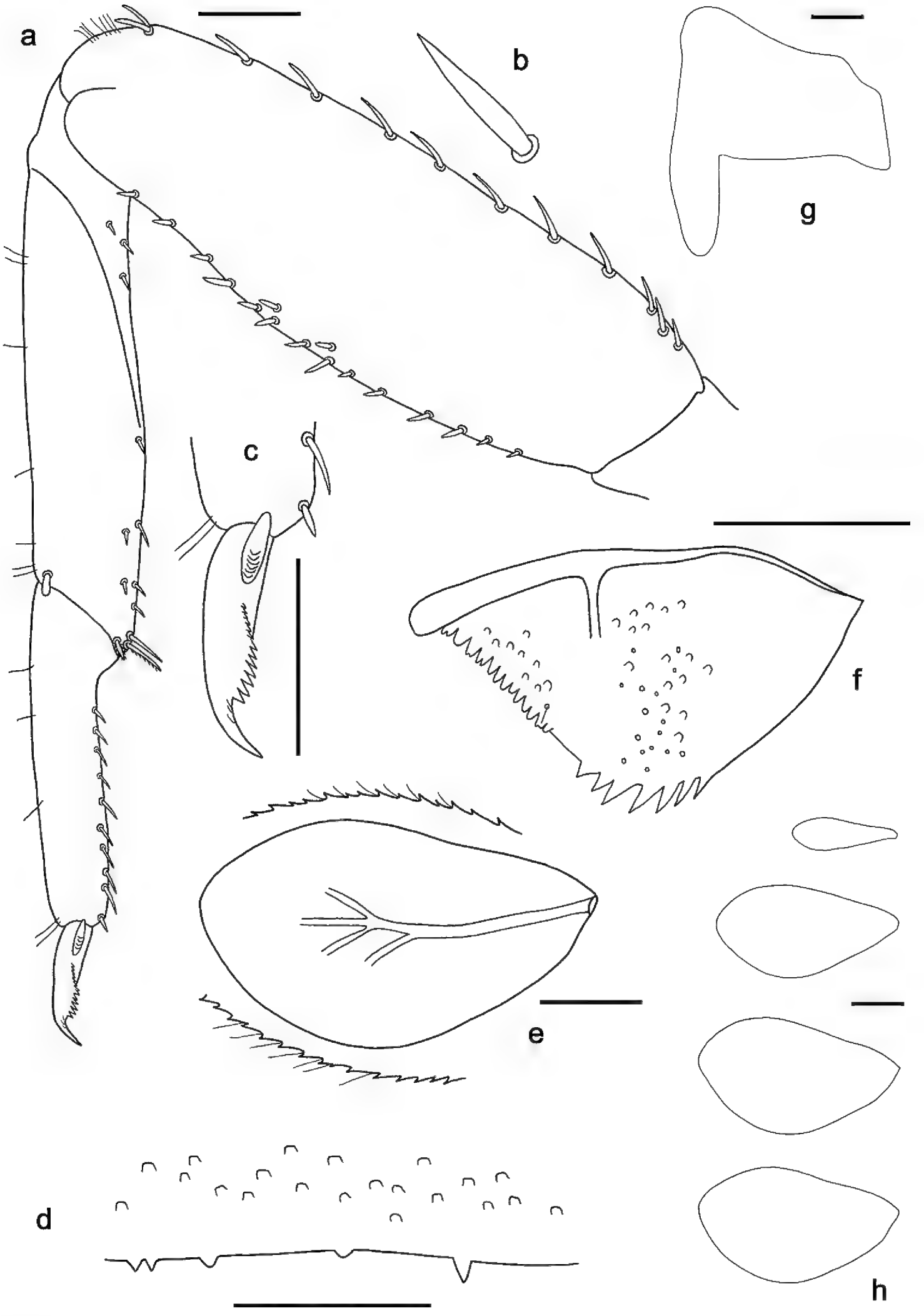


Figure 12. *Nigrobaetis richardi* sp. nov., nymph morphology: **a** foreleg **b** seta at dorsal margin of femur **c** fore claw **d** tergum IV **e** gill IV **f** paraproct **g** metanotum (left side), with hind protopteron (mature nymph) **h** gills I, II, III, IV (top to down). Scale bars: 0.1 mm.

Middle and hind legs. As foreleg, but tibia dorsally with row of spine-like setae.

Terga (Fig. 12d). Surface scattered with U-shaped scale bases. Posterior margin of terga I–III without spines; posterior margin of terga IV and V partly with some rudimentary, triangular spines; posterior margin of terga VI–IX with medial, triangular spines, longer than wide.

Gills (Fig. 12e, h). Present on segments I–VII. Margin with small denticles intercalating short, fine simple setae. Tracheae only partly extending to inner and outer margins. Gill I as long as 2/3 of segment II; gill IV as long as length of segments V and 1/3 VI combined; gill VII as long as length of segments VIII and 2/3 IX combined.

Paraproct (Fig. 12f). Distally not expanded, with 5–7 marginal spines. Surface scattered with U-shaped scale bases and micropores. Cercotractor with small, marginal spines.

Etymology. Dedicated to the late entomologist Barton A. Richard (formerly Florida A&M University, Tallahassee), who participated in an early phase of this project (2004–2007).

Distribution (Fig. 13). Comoros (Anjouan).

Biological aspects. The specimens were collected at altitudes of 210 m and 600 m, together with *L. glaucus*, *L. vinosus* and *P. freitagae*. The characteristics and environmental conditions of the sampling sites in the Comoros (Anjouan, Riv. Tatinga) are described in Starmühlner (1979: pp. 652, 655): river width 3–10 m, depth 5–50 cm, water temperature 22 °C–24.5 °C, bottom substrata consisted of basaltic rock, boulders, gravel and sand.

Type material. ***Holotype.*** Comoros • nymph; Anjouan, Riv. Tatinga, upper course, near Dindri; 600 m; 11.03.1974; leg. F. Starmühlner; on slide; GBIFCH00515655; MZL. ***Paratypes.*** Comoros • 3 nymphs; Anjouan, Riv. Tatinga, lower course, by the bridge; 210 m; 22.03.1974; leg. F. Starmühlner; 2 on slides; GBIFCH00592759, GBIFCH00592715, GBIFCH00592716; MZL, 1 in alcohol; GBIFCH00515656; FAMU.

7. *Potamocloeon* (*Aquaediva*) *freitagae* (Gattolliat, 2001)

Figures 10b, 13, 14

Potamocloeon freitagae: Gattolliat 2001a: figs 13–19.

Diagnose. Nymph. Following combination of characters: A) labrum on dorsal surface with a long, simple submedian seta and a submarginal arc of simple setae; B) both mandibles with long, stout setae between prostheca and mola, incisors blade-like; C) labial palp without protuberance at segment II; D) legs stocky with tibia and tarsus almost fused; tibia and tarsus with subproximal arc of long, fine, simple setae; claw short, without denticles.

Complementary description. Nymph (Figs 10b, 14). Body length 3.8–4.8 mm (up to 5.5 mm according to Gattolliat 2001a). Cerci: ca. 2/3 of body length. Paracercus: ca. 3/4 of cerci length. Antenna: approx. 1.5× as long as head length.

Colouration (Fig. 10b). See also Gattolliat 2001a, colouration may be altered due to long storage of nymphs in alcohol. Head, thorax and abdomen dorsally brown, ab-

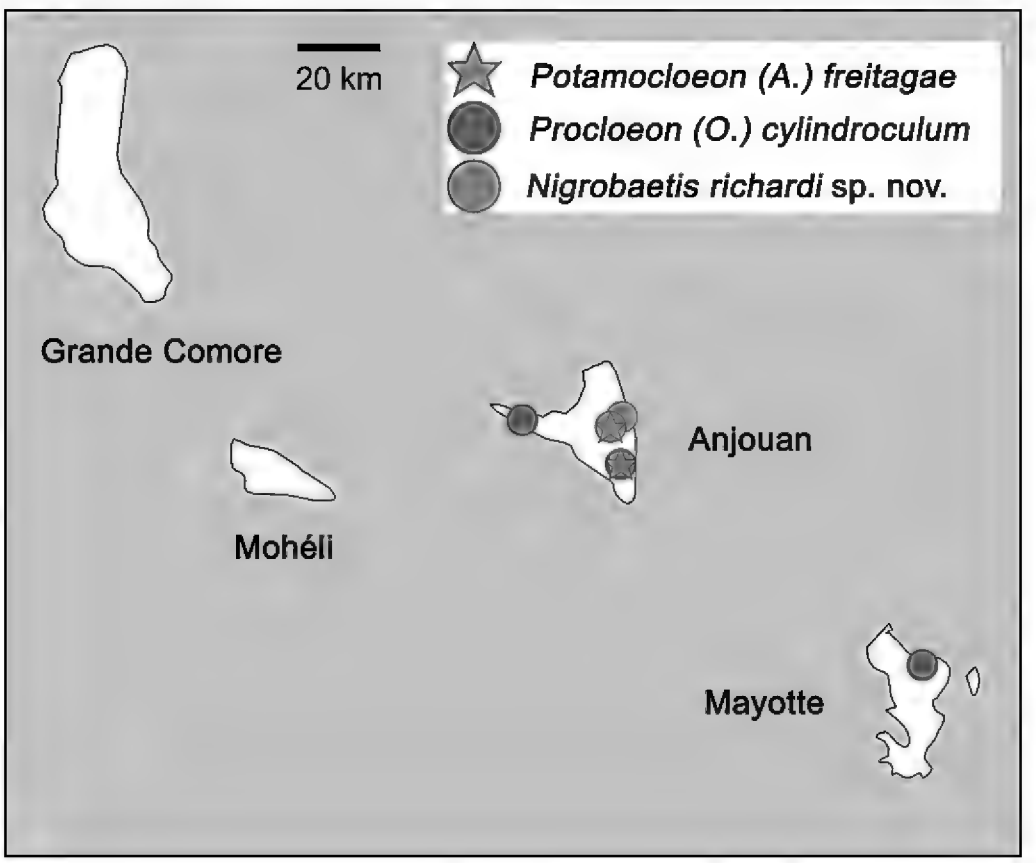


Figure 13. Distribution of *Nigrobaetis richardi* sp. nov., *Potamocloeon* (*A.*) *freitagae* and *Procloeon* (*O.*) *cylindroculum* in the Comoros Archipelago.

dominal segments V and VI darker; head, thorax and abdomen ventrally light brown. Legs light brown, caudalii light brown.

Right mandible (Fig. 14a, b). Incisor and kinetodontium partly fused. Incisor blade-like; kinetodontium with three denticles. Prostheca stick-like, apically with two long and several short denticles. Margin between prostheca and mola straight, with long, stout setae. Tuft of setae at apex of mola present.

Left mandible (Fig. 14c, d). Incisor and kinetodontium partly fused. Incisor blade-like; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with long, stout setae. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola absent.

Hind protoptera (Fig. 14e) vestigial or absent.

Gills (Fig. 14f–l). Present on segments I–VII. Tracheae extending to inner and outer margins. Gill I as long as segment II; gill IV as long as segments V, VI and VII combined; gill VII nearly reaching bases of cerci.

Distribution (Fig. 13). Comoros (Anjouan), Madagascar.

Biological aspects. The specimens were collected at altitudes of 600 m and 750 m, together with *A. bicorne* and *N. richardi* sp. nov.. The characteristics and environmental conditions of the sampling sites in the Comoros (Anjouan: Riv. Tatinga, Riv. Santsa) are described in Starmühlner (1979: pp. 651, 652): river width 0.5–8 m, depth 2–50 cm, water temperature 22 °C–24 °C, bottom substrata consisted of basaltic rock, boulders, gravel and sand.

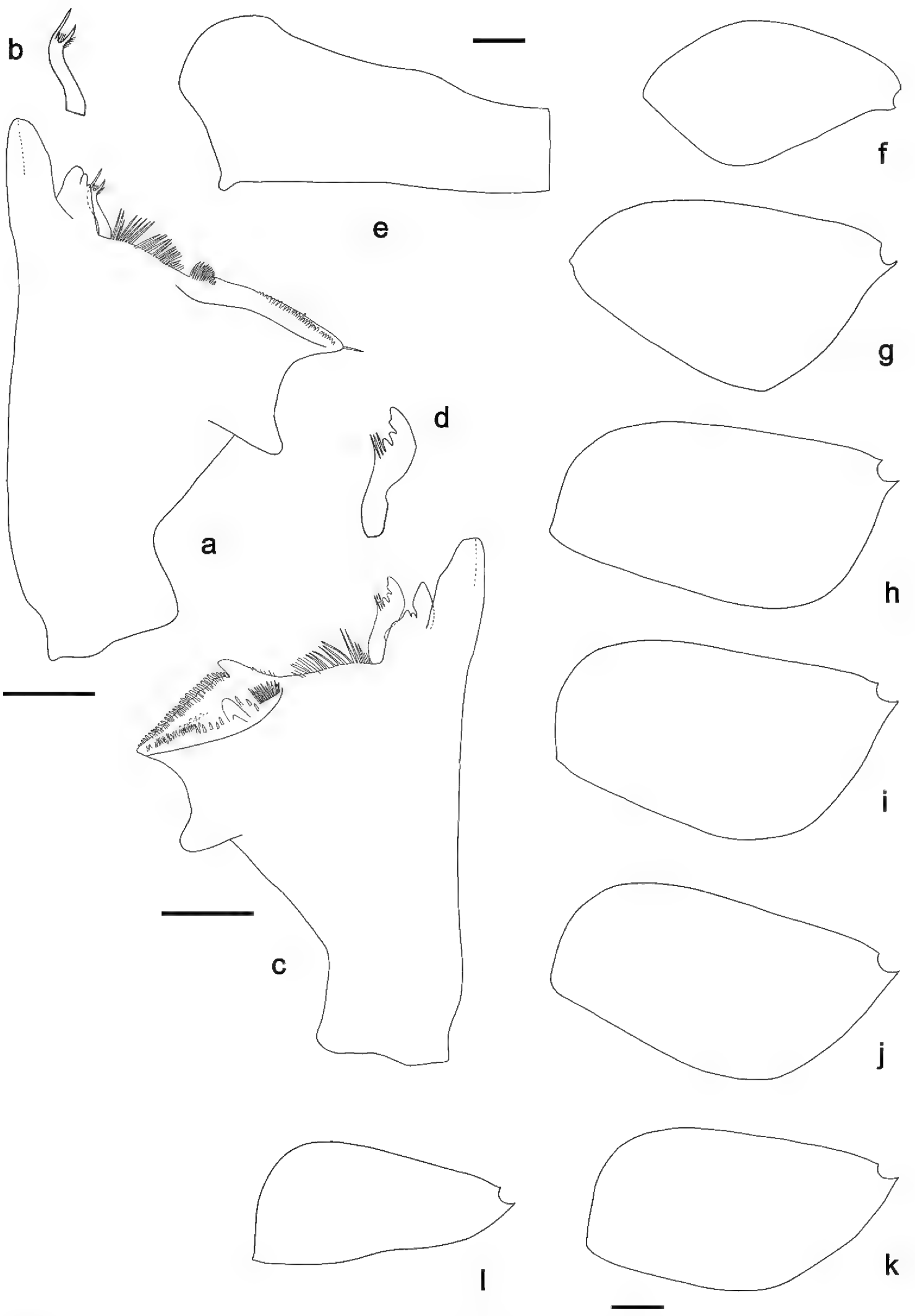


Figure 14. *Potamocloeon* (*A.*) *freitagae*, nymph morphology: **a** right mandible **b** right prostheca **c** left mandible **d** left prostheca **e** metanotum (left side), with minute hind protopteron (mature nymph) **f** gill I **g** gill II **h** gill III **i** gill IV **j** gill V **k** gill VI **l** gill VII.

Material examined. Comoros • 5 nymphs; Anjouan, Riv. Tatinga, upper course, near Dindri; 600 m; 11.03.1974; leg. F. Starmühlner; 4 on slides; GBIFCH00592753, GBIFCH00515707, GBIFCH00592725, GBIFCH00592709, GBIFCH00592712, GBIFCH00592710; 1 in alcohol; GBIFCH00515659; MZL, FAMU • 2 nymphs; Anjouan, Riv. Santsa, upper course, near Adda-Douéni; 750 m; 21.03.1974; leg. F. Starmühlner; 1 on slide; GBIFCH00592754; 1 in alcohol; GBIFCH00515660; MZL, FAMU.

8. *Procloeon* (*Oculogaster*) *cylindroculum* Kimmins, 1956

Procloeon (*O.*) *cylindroculum*: Kluge 2016: figs 1–29.

Diagnosis. Nymph. Following combination of characters: A) maxillary palp 2-segmented; B) labial palp with enlarged, falcate segment III; C) claw elongate, with two rows of denticles, minute in proximal part and larger in proxomedial part; D) hind protoptera absent; E) seven pairs of gills, gills I–V or I–VI with two lamellae, upper lamella much narrower than lower one; F) laterally strong, pointed spines at least on abdominal segments V–IX; G) paracercus subequal to cerci.

Distribution (Fig. 13). Gambia, Ghana, Mali, South Africa, Tanzania, Uganda, Zambia, Zimbabwe (Kluge 2020, 2021).

Biological aspects. In the Comoros, the specimens were collected at altitudes of 150 m and 750 m, partly together with *A. bicorne*. The characteristics and environmental conditions of the sampling sites (Anjouan, Riv. Foumbani, Riv. Santsa) are described in Starmühlner (1979: pp. 651, 656): river width 0.5–2 m, depth 1–10 cm, water temperature 24 °C–26 °C, bottom substrata consisted of basaltic rock, boulders, stones, gravel and sand. In Mayotte, the specimens were collected at an altitude of 30 m, together with *D. mayottensis* sp. nov. and *L. glaucus*.

Material examined. Comoros • 2 nymphs; Anjouan, Riv. Foumbani, Foumbani, near Sima; 150 m; 26.03.1974; leg. F. Starmühlner; 1 on slide; GBFCH00592756; 1 in alcohol; GBIFCH00515657; MZL • 2 nymphs; Anjouan, Riv. Santsa, upper course, near Adda-Douéni; 750 m; 21.03.1974; leg. F. Starmühlner; 1 on slide; GBIFCH00592755; 1 in alcohol; GBIFCH00515658; FAMU. Mayotte • 1 nymph; Riv. Longoni, Loc. Longoni aval; 12°44'20"S, 45°09'53"E; 30 m; 14.05.2006; leg. N. Mary; on slide; GBIFCH00592750; MZL • 2 nymphs; Riv. Longoni, Loc. Longoni aval; 12°44'20"S, 45°09'53"E; 30 m; 16.04.2009; leg. N. Mary; 1 on slide; GBIFCH00592717; 1 in alcohol; GBIFCH00515725; MZL.

Key to the Baetidae species of the Comoros and Mayotte (nymphs)

1 Legs stocky with tibiae and tarsi almost fused, claws short and without denticles..... ***Potamocloeon* (*A.*) *freitagae***

– Legs elongated with free tibiae and tarsi, claws with denticles **2**

2 Claws elongated, with numerous denticles; at least part of the gills formed by two lamellae; abdominal segments VI–IX laterally with strong, apically pointed spines **3**

– Claws not elongated, with less than 15 denticles; all gills formed by a single lamella; abdominal segments VI–IX laterally without spines **4**

3 Upper lamella of gills rounded, almost as developed as lower one ..... ***Cloeon smaeleni***

– Upper lamella of gills elongated, sometimes as long as lower one, but much narrower ..... ***Procloeon* (*O.*) *cylindroculum***

4 Antennae close to each other with small carina in between; posterior margin of tergite IV with discontinuous row of few reduced, triangular spines (Fig. 12d) ..... ***Nigrobaetis richardi* sp. nov.**

– Antennae without carina in between; posterior margin of tergite IV with continuous row of triangular spines **5**

5 Labial palp segment II with large distomedial protuberance; maxillary palp segment II with distolateral excavation; mandibles without setae between prostheca and mola; fore tibia with patellotibial suture (*Labiobaetis*) **6**

– Labial palp segment II without distomedial protuberance; maxillary palp segment II without excavation; at least right mandible with setae between prostheca and mola; fore tibia without patellotibial suture (Protopatellata) 7

6 Seven pairs of gills; hind protoptera well developed ..... ***Labiobaetis glaucus***

– Six pairs of gills; hind protoptera absent or vestigial ..... ***Labiobaetis vinosus***

7 Incisor of both mandibles blade-like, kinetodontium with denticles (Fig. 6b, d); tibia with an arc of long, fine, simple setae (Fig. 7a); claw with one row of denticles, without subapical setae (Fig. 7b) ..... ***Dabulamanzia mayottensis* sp. nov.**

– Incisor and kinetodontium of both mandibles with denticles (Fig. 3b, d); tibia without arc of fine, simple setae; claw with two rows of denticles and a pair of subapical setae (Fig. 4a, b) ..... ***Afroptilum bicorne***

Discussion

Afroptilum bicorne

Ulmer (1909) described this species as *Centroptilum bicorne* from the island of Mohéli (Comoros), based on imagos only. Later, Gillies (1990) transferred it to the new genus *Afroptilum* Gillies, 1990. Additionally, he included it in the *A. sudafricanum* species group, characterized by a forewing with single intercalary veins and a double-spurred hindwing of the adult and potentially the cap-like labial palp segment III of the nymph. However, Ulmer (1909: fig. 2) also depicted the male gonostyli, which do not have the shape typical for *Afroptilum*, with an elongate and not globular segment III (Gillies 1990). To the contrary, this drawing is very similar to the gonostyli of *Labiobaetis glaucus* (see Gattolliat et al. 2018: fig. 46), with segment I and II almost fused, a trian-

gular, well-marked expansion at segment I and segment III almost globular. *Labiobaetis glaucus* is very frequent in Anjouan and also in Mayotte and there is no reason to assume that it is not present in Mohéli too. The material used by Ulmer (1909) for the description was in poor condition, he had only two males, one of which without wings. Therefore, he was not able to assign the latter to the new species with certainty. The most probable hypothesis is that the two male imagos did not belong to the same species: the one with forewings belongs to *Afroptilum bicorne* while the one used for the drawing of the gonostyli belongs to *Labiobaetis glaucus*. Because of the poor state of the material, Ulmer did not notice that the two imagos are not conspecific.

The nymph described in this study (Figs 2a, 3, 4) is very close to *A. sudafricanum* (Lestage, 1924), with the cap-like labial palp segment III typical for the genus, the mandibles with stout setae between prostheca and mola on both sides, and a claw with two rows of denticles and a pair of subapical setae (Figs 3i, 4b). Moreover, the protogonostyli developing under the cuticle of male last instar nymphs are folded in the *Afroptilum* type (Kluge 2004: fig. 29E). The main differences between the two species are a minute, sharp process at the inner base of labial palp segment III, absent in *A. sudafricanum*, the number of setae at the dorsal margin of the femur (ca. 21 in *A. sudafricanum*; ca. 30 in *A. bicorne*), and a long, stout seta distomedially at the ventral margin of the tibia (present in *A. sudafricanum*; absent in *A. bicorne*) (Fig. 3a, i; Kluge 2004: fig. 28C; nymph from South Africa, Reg. Winterberg, 09.2007, GBIFCH00592724). The sharp process at labial palp segment III of *A. bicorne* is always clearly visible in the specimens from Anjouan (Comoros), but poorly developed in the specimens from Mayotte. Therefore, we recommend verifying the assignment of the specimens from Mayotte to *A. bicorne* by genetics with fresh material from the Comoros in the future.

The Comoros are poorly diversified and no other *Afroptilum* sp. was found so far. We therefore reasonably assume that the nymphs from Anjouan belong to the same species, *A. bicorne*, as the male imago described by Ulmer (1909) from the close neighbouring island of Mohéli.

Arimoro and Muller (2010) reported *A. bicorne* from Nigeria in an ecological study. However, it is unclear how the identification and the difference to *A. sudafricanum* were done. The literature cited for that purpose is not suitable for this task. We consider this report to be very doubtful and see a high probability that the species from Nigeria is actually *A. sudafricanum* or another species of *Afroptilum*.

Dabulamanzia mayottensis sp. nov.

The genus *Dabulamanzia* Lugo-Ortiz & McCafferty, 1996, was established based on two autapomorphies (the bulbous segment III of labial palps and the small, basomedial projection of segment II of the male gonostyli) and a combination of other characters (e.g. incisor and kinetodontium of the right mandible being united for nearly two thirds of their length; proximal arc of long, fine, simple setae on the tibia) (Lugo-Ortiz and McCafferty 1996). *D. mayottensis* sp. nov. is only known from nymphal stage; it shares the characters of the right mandible and the arc of long, fine, simple setae on

the tibia with *Dabulamanzia*, the bulbous shape of segment III of the labial palp is rather poorly expressed; and it is in nearly all characters (incl. labial palp segment III) very similar to *D. concolorata* Gattolliat, 2000, from Madagascar. Therefore, we assign this new species to *Dabulamanzia*. Both species can be easily distinguished by the shape of the labrum: the labrum of *D. concolorata* is less wide with a length of 0.8× maximal width (Gattolliat and Sartori 2000: fig. 19); the labrum of *D. mayottensis* sp. nov. is clearly wider with a length of 0.7× maximal width (Fig. 6a). All other species of *Dabulamanzia* are different from these two species by the more bulbous labial palp segment III and partly by the mandibles (incisors or prostheca).

However, for both *D. concolorata* and *D. mayottensis* sp. nov., the arc of long, fine, simple setae on the tibia is not short (as described for the genus by Lugo-Ortiz and McCafferty 1996), but long, reaching around the dorsal margin till the posterior side (Fig. 7a). On the foreleg, it follows the line of the former patellotibial suture; on middle and hind leg, it goes along with the patellotibial suture. This character is similar in the Malagasy species *D. improvida* Lugo-Ortiz & McCafferty, 1997, *D. gladius* Gattolliat, 2000 and *D. gigantea* Gattolliat, 2000, and in *Dabulamanzia* spp from South Africa and Ivory Coast. Probably, this character was misinterpreted in previous studies (Lugo-Ortiz and McCafferty 1996; Gattolliat and Sartori 2000) and is similarly present in all species of *Dabulamanzia*.

Dabulamanzia mayottensis sp. nov. is frequent and widespread in Mayotte, but it seems that it has never reached other islands of the Comoros archipelago, based on the limited collections done in the Comoros so far.

Labiobaetis glaucus and *L. vinosus*

The Panafrotropical species *L. glaucus* was already reported for Mayotte based on morphology and genetic evidence (COI; Gattolliat et al. 2018). It is the most widespread and frequent mayflies species of the Comoros archipelago; in Mayotte it is often found together with the similarly frequent *D. mayottensis* sp. nov. However, it is absent in Madagascar, a well-studied island (Gattolliat 2001b). In Anjouan (Comoros), it was partly collected together with *L. vinosus*, another Panafrotropical species. Only a few specimens of *L. vinosus* were identified from a single river in Anjouan, but it may have been overlooked sometimes in the middle of the much more frequent *L. glaucus*. It is very difficult to distinguish *L. vinosus* morphologically from *L. vulgaris* Gattolliat, 2001, a species rather abundant in Madagascar. However, an interspecific genetic difference (rRNA) between both species was calculated by Monaghan et al. (2005). One of the specimens from the Comoros (GBIFCH00592719) has minute hind protoptera and *L. vinosus* may have such minute hind protoptera or they are completely absent (Kaltenbach and Gattolliat 2021). In *L. vulgaris*, minute hind protoptera were not seen so far and not described (Gattolliat 2001b). Further, we did not find *L. vinosus* on the relatively well-sampled Mayotte, which is closer to Madagascar. Therefore, we conclude that the species from Anjouan belongs most probably to the Panafrotropical *L. vinosus*.

Nigrobaetis richardi sp. nov.

Nigrobaetis richardi sp. nov is showing the usual combination of nymphal characters for this genus: antennae standing closely together, with a keel between them; labrum with a submarginal arc of one plus two long, simple, stout setae on dorsal surface, and several shorter, stout, simple setae just below; mandibles with stout setae between prostheca and mola; labial palp segment II without protuberance (Fig. 11a, b, d, h). Species of *Nigrobaetis* Kazlauskas (in Novikova and Kluge), 1987 may be often distinguished by the combination of the number of pairs of gills and the presence or absence of hind protoptera. *Nigrobaetis richardi* sp. nov. has seven pairs of gills and well developed hind protoptera. From the Afrotropical species we can already exclude *N. colonus* Gattolliat, 2004 (La Réunion), *N. cryptus* Gattolliat, 2004 (Madagascar), *N. bethuneae* Lugo-Ortiz & de Moor, 2000 (Southern Africa) and *N. harasab* Soldan, 1977 (Sudan) based on these characters. Other Afrotropical species (and from neighboring areas) with seven pairs of gills and hind protoptera are *N. vuatazi* Gattolliat & Sartori, 2012 (Jordan), *N. arabiensis* Gattolliat & Sartori, 2008 (UAE) and *N. numidicus* Soldán & Thomas, 1983 (Algeria). The first two species are differentiated by their stocky tibiae and the last one by the absence of setae between prostheca and mola of the right mandible (Soldán and Thomas 1983; Gattolliat and Sartori 2008; Gattolliat et al. 2012). Further, they have either full grown triangular spines at posterior margin of tergite IV or no spines, and *N. richardi* sp. nov. has rudimentary spines (Fig. 12d). *Nigrobaetis gracilis* Bogoescu & Tabacaru, 1957 (Europe, Caucasus, Turkey, Iran) has the most similar morphology to *N. richardi* sp. nov., but also some clear differences based on the description in Müller-Liebenau (1969: p. 179, figs 140g, h, 141): forefemur with 19–21 stout, clavate, apically serrate setae at the dorsal margin, less at the middle femur and only seven or eight at the hind femur (*N. richardi* sp. nov. has 8–10 lanceolate, pointed setae at the dorsal margin of all legs; Fig. 12a, b); tibia with row of stout, clavate, apically serrate setae at dorsal margin (*N. richardi* sp. nov. with only fine, simple setae; Fig. 12a); tergites at posterior margin with long, triangular spines (*N. richardi* sp. nov. with rudimentary spines at tergites IV and V and without spines at tergites I–III; Fig. 12d).

Potamocloeon (Aquaediva) freitagae

Remarkably, the Malgasy *P.* (*A.*) *freitagae* was also collected in Anjouan (Comoros), but not in the much better sampled Mayotte, which is closer to its type locality. From Madagascar, it was reported from the northernmost end of the island only, living in pools of small streams (JLG, personal observation). Therefore, it is possible that it lives in microhabitats that were not sampled in Mayotte during the long-term repetitive monitoring of freshwater quality based on strict protocols. Additional sampling in Mayotte, including pools of small streams, would be necessary to answer this question.

A thorough comparison of the specimens from Comoros with the type series from Madagascar did not reveal any morphological differences. Nevertheless, we rec-

ommend comparing the genetics (COI barcodes) of both populations with new material in the future, especially, if the species is not found on Mayotte at a later point in time.

In the original description of *P.* (*A.*) *freitagae* (Gattolliat 2001a), the mandibles were indicated as similar to *P.* (*A.*) *bicoloratum*, based on specimens on slides, which all had strongly worn mandibles. Based on the material from the Comoros, we redescribe the mandibles (see above): the incisors of both mandibles are blade-like without denticles in *P.* (*A.*) *freitagae* (Fig. 14a, b), but do have denticles in *P. bicoloratum* (Gattolliat 2001a: figs 3a, 4). In worn condition, they look the same in both species. In Madagascar, *Potamocloeon* (*Aquaediva*) *pseudogladium* (Gattolliat, 2001) also presents bladelike mandibles, but in this species both prosthecas are sticklike and the labrum is very broad (Gattolliat 2001a). We found minute hind protoptera in one specimen of *P.* (*A.*) *freitagae* (Fig. 14e), which probably is an unstable character.

Procloeon (*Oculogaster*) *cylindroculum*

Kluge (2016, 2020) reviewed the situation in this genus, described the subgenus *Oculogaster* Kluge, 2016, and assigned to it, amongst others, two new species from South Africa. *Procloeon* (*O.*) *cylindroculum* can be distinguished from *P.* (*O.*) *barnardi* Kluge, 2020 only by the colouration of the winged stages (Kluge 2020), but we only have nymphs from the Comoros and Mayotte. Therefore, the specific assignment remains provisional. However, *P.* (*O.*) *cylindroculum* is a Panafrotropical species while *P.* (*O.*) *barnardi* is known from South Africa only (Kluge 2020). Therefore, we make the reasonable assumption that the specimens from the Comoros and Mayotte belong to *P. cylindroculum*. The genus *Procloeon* Bengtsson, 1915 is not present in Madagascar.

Biogeography

The Comoros archipelago expands nearly half way between the African continent and the island of Madagascar and thus could have served as stepping stones for a faunal exchange between Africa and Madagascar in both directions. The distribution and morphological affinities of the Baetidae may contribute to understand the colonisation history in this region. Some of them are probably African faunal elements: the nymph of *A. bicorne* is most similar to the African *A. sudafricanum*; the Panafrotropical *L. glaucus* is absent in Madagascar; the equally Panafrotropical *L. vinosus* is absent in Mayotte and Madagascar, but *L. vulgaris* is the sister-species in Madagascar and may be potentially derived from an ancient colonisation of the island by *L. vinosus*; the Panafrotropical *P.* (*O.*) *cylindroculum* is present in the Comoros and Mayotte, but the genus is absent in Madagascar. Other Baetidae have probably a Malagasy origin: *D. mayottensis* sp. nov. is limited to Mayotte and its nymphal morphology is most similar to *D. concolorata* from Madagascar; *P.* (*A.*) *freitagae* is distributed in northernmost Madagascar and in the Comoros. *Cloeon smaeleni* is a special case: it has a vast Afrotropical distribution, and is

very successful in colonisation, being also present in Madagascar, La Réunion, and recently even in Brazil. It remains unclear, which way this species arrived in the Comoros archipelago. As a conclusion, the Baetidae fauna of the Comoros archipelago has affinities to Africa as well as to Madagascar and the colonisation of the volcanic islands most probably happened from both origins. This is in line with the results of a genetic study of Afrotropical Baetidae including Madagascar by Monaghan et al. (2005): several lineages contained sister taxa on the African continent and in Madagascar and the relationships range from very recent dispersal to ancient vicariance. Dispersal was most recent and frequent in species that spend the nymphal stage in lentic water, e.g. *Cloeon* sp. The trans-oceanic faunal exchange between Africa and Madagascar was most probably bi-directional.

Based on this study and other studies in the past, the mayfly fauna of the Comoros archipelago seems to be poor. Mayotte is well sampled due to the long-term and still ongoing freshwater monitoring program, contrary to the Comoros, where collection activities remained very limited in the past. Mohéli was not sampled for more than a century, the fauna of this island remains virtually unknown apart from the original report of *A. bicorne*. Additionally, there is no natural water course on the main island Grande Comore, but only artificial cisterns and water reservoirs with stagnant water. Therefore, we may reasonably assume that only very few additional species will be found in this archipelago with further collections in the future.

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